THE COCHLEAR DUCT OF SNAKES[1]

By

Malcolm R. Miller

*Department of Anatomy, University of California School of Medicine,
and Department of Herpetology, California Academy of Sciences,
San Francisco, California*

Drawings by WAYNE EMERY, *Department of Medical
Illustration, and technical assistance by* MICHIKO KASAHARA
*Department of Anatomy, University of California School of Medicine,
San Francisco*

INTRODUCTION

The origin of snakes, and the classification of modern snakes as well, are problems of concern and dispute. While it is generally accepted that snakes probably arose from a lizard-type ancestor, there is no general agreement concerning the specific characteristics of the progenitor. Excellent and concise accounts of the problems of snake origins and classification have been published by Underwood (1967) and Bellairs and Underwood (1951).

Dowling (1959), as well as Underwood (1967), aptly point out that a good deal of the difficulty in classifying snakes is a simple insufficiency of anatomical information. While studies of a variety of anatomical systems have contributed to the understanding of ophidian relationships, further and much more comprehensive investigations are much needed.

One might not suspect that a study of the detailed anatomy of the various organs of special senses would be helpful in the solution of taxonomic problems. However, the provocative results of Walls' (1942) study of the reptilian eye, illustrates well the taxonomic value of comparative studies of the sensory system.

[425]
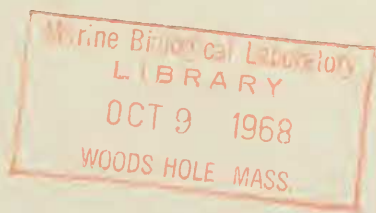
Further, Shute and Bellairs in 1953 made a most valuable contribution in demonstrating that the lizard cochlear duct was of potential taxonomic utility. This observation was later confirmed and extended by the studies of Baird (1960), Hamilton (1964), and Schmidt (1964). In part, because of my interest in the evolution of the vertebrate auditory system, I undertook a comprehensive study of the gross and histological anatomy of the lizard cochlear duct. In 1966 (Miller, 1966a) I published an account covering some one-third of the living genera of lizards. Later (Miller, 1966c) the results of a study of the anatomy of the ducts of *Lanthanotus* and *Anelytropsis* were reported.

The essential fact about the lizard cochlear duct is that it is anatomically distinct in each family of living lizards, and in addition, the ducts of closely related families are structurally similar to one another. Thus, it was with great anticipation that I began a study of the snake cochlear duct hoping that I might find clues as to which group of lizards, snakes might be most closely related, or, answer some of the perplexing problems concerning the relationships of some of the various types of colubrid snakes to one another. A preliminary report on the anatomy of the snake cochlear duct has been published (Miller, 1966b).

Materials and Methods

Most twentieth-century anatomists have studied the vertebrate membranous labyrinth by means of serial sections and reconstructions (de Burlet, 1934; Baird, 1960; Hamilton, 1964). While I, too, began my studies in this way, I found by experimentation that the intact cochlear duct of lizards could be removed easily from its bony housing and the anatomical detail studied by direct observation. Further, the membranous labyrinths of museum preserved specimens were usually well enough preserved to be useful for gross anatomical study.

The combination of being able to dissect the cochlear duct free from the otic capsule together with the availability of the large herpetological collection of the California Academy of Sciences thus enabled me to study a large variety of reptilian cochlear ducts in a relatively short time span. If one studies carefully the illustrations in the earlier studies of the vertebrate cochlear duct by several nineteenth-century anatomists [Retzius (1884), Hasse (1873), and Kuhn (1882)], it is apparent that these anatomists studied the membranous labyrinth by gross dissection of the otic capsule.

The present paper presents the results of a study of the cochlear duct of 200 genera of living snakes and includes representatives of all recognized families and most of the currently recognized subfamilies (Underwood, 1967). The species studied are listed in table I.

The intact cochlear duct was obtained from the animals in the following manner: 1) The skin over the temporal region of the head was incised, dissected free from the underlying fascia and folded downwards to form a three-sided flap.

TABLE I. *List of materials examined.*

I. Primitive Families

    A. Aniliidae

        Anilius scytale   (CAS 39264 [501])[3]
        Cylindrophis rufus   (CAS 33053 [264])

    B. Uropeltidae

        Platypectrurus madurensis   (SU 9114 [478])[4]
        Plectrurus aureus   (CAS 17176 [551])
        Rhinophis oxyrhynchus   (CAS 39619 [650])

    C. Loxocemidae

        Loxocemus bicolor   (SU 16206 [416])

    D. Xenopeltidae

        Xenopeltis unicolor   (SU 7278 [444])

    E. Typhlopidae

        Liotyphlops caracasensis   (CAS 44619 [642])
        Typhlops australis   (AM 6425 [719])[5]
        Typhlops australis   (AM 6416 [720])
        Typhlops bituberculatus   (AM R13424 [721])
        Typhlops bituberculatus   (AM R6406 [722])
        Typhlops braminus   (CAS 101599)
        Typhlops lumbricalis   (CAS 71784 [177])
        Typhlops nigrescens   (CAS 84095 [138])
        Typhlops nigrescens   (AM 10373 [717])[5]
        Typhlops nigrescens   (AM 10288 [718])
        Typhlops proximus   (AM R14946 [714])
        Typhlops proximus   (AM R13661 [715])
        Typhlops proximus   (AM R13779 [716])
        Typhlops punctatus   (CAS 55104 [176])

    F. Leptotyphlopidae

        Leptotyphlops humilus   (CAS 80433 [586])
        Leptotyphlops humilus   (CAS   [587])

II. Boidae

        Calabaria reinhardti   (CAS 16960 [502])
        Charina bottae   (CAS 28326 [265])
        Chondropython viridis   (CAS 39988 [661])
        Constrictor constrictor   (CAS 97383 [408])
        Constrictor constrictor   (CAS 97368 [602])
        Enygrus carinatus   (CAS 72039 [263])
        Epicrates exsul   (SU 21669 [419])
        Eryx conica   (CAS 99810 [392])
        Eryx johni   (CAS   [355])[6]

[3] The first number is the California Academy of Sciences, Department of Herpetology catalogue number of the specimen. The number in brackets is the catalogue number of the cochlear duct which is preserved separately in the collections of the Department of Herpetology of the Academy.
[4] Stanford University, Division of Systematic Biology catalogue number.
[5] Australian Museum, Sydney, Australia, catalogue number.
[6] Uncatalogued fresh specimen, cochlear duct only, preserved.

Table I. *Continued.*

II. Boidae (continued)

Eryx johni	(CAS [397])
Eunectes murinus	(CAS 93200 [656])
Liasis childreni	(CAS 77804 [639])
Lichanura roseofusca	(SU 18288 [429])
Lichanura roseofusca	(CAS 58114 [403])
Python molurus	(CAS [388])
Python reticularis	(CAS 15187 [271])
Tropidophis melanurus	(CAS 100450 [601])

III. Colubridae

Abastor erythrogrammus	(CAS 43634 [611])
Acrochordus granulatus	(CAS 15189 [270])
Acrochordus granulatus	(SU 23700 [417])
Acrochordus granulatus	(SU 23701 [418])
Acrochordus javanicus	(CAS 16856 [612])
Ahaetulla prasina	(SU 21039 [413])
Alsophis vudii	(CAS 39318 [571])
Aplopeltura boa	(CAS 15350 [646])
Aparallactus capensis	(CAS 85965 [638])
Arizona elegans	(CAS 84139 [594])
Boiga irregularis	(CAS 49911 [560])
Calamaria gervaisi	(SU 23149 [410])
Carphophis amoenus	(CAS 71622 [564])
Cemophora coccinea	(CAS 38765 [595])
Cerberus rhynchops	(SU 18791 [412])
Chilomeniscus cinctus	(CAS 91244 [561])
Chionactis occipitalis	(SU 19893 [427])
Chlorophis irregularis	(CAS 39263 [598])
Chrysopelia ornata	(SU 18446 [426])
Chrysopelia paradesi	(CAS 15330 [579])
Coluber constrictor	(CAS 29496 [662])
Coluber gemonensis	(CAS 17000 [636])
Coniophanes punctigularis	(CAS 66422 [634])
Contia tenuis	(CAS 28317 [269])
Coronella austriaca	(CAS 17088 [621])
Crotaphopeltis hotamboeia	(CAS 38731 [626])
Cyclocorus lineata	(SU 18885 [411])
Dasypeltis scabra	(CAS 85300 [584])
Dendrelaphis boiga	(SU 18448 [462])
Dendrelaphis caudolineatus	(SU 23445 [414])
Diadophis amabilis	(CAS 13370 [268])
Dispholidus typus	(CAS 85783 [576])
Dromicus hoodensis	(CAS 11924 [597])
Dryadophis melanolomus	(CAS 95762 [629])
Drymarchon corais	(CAS 96886 [622])
Drymobius margaretiferus	(SU 23797 [541])
Duberria lutrix	(CAS 85896 [624])

TABLE I. *Continued.*

III. Colubridae (continued)

Elaphe obsoleta	(CAS 33200 [273])
Elaphe quadrivirgata	(CAS 15950 [658])
Enhydris pakistanica	(CAS [402])
Farancia abacura	(SU 9036 [546])
Ficimia olivacea	(CAS 100081 [616])
Geophis nasalis	(CAS 66720 [635])
Gonyosoma oxycephalum	(CAS 61832 [625])
Haldea striatulata	(CAS 73992 [607])
Helicops angulatus	(CAS 49325 [655])
Herpeton tentaculatum	(CAS 101602 [589])
Herpeton tentaculatum	(CAS [605])
Herpeton tentaculatum	(CAS 101520 [608])
Heterodon platyrhinus	(CAS 33272 [600])
Hologerrhum philippinum	(CAS 61554 [618])
Homalopsis buccata	(CAS 85302 [590])
Hypsiglena torquata	(CAS 91438 [620])
Imantodes gemmistratus latistratus	(SU 23823 [422])
Lampropeltis getulus	(CAS [129])
Lampropeltis getulus	(CAS 62931 [654])
Leptodeira punctata	(SU 23909 [545])
Leptophis species	(SU 23593 [544])
Liodytes alleni	(CAS 63091 [623])
Lioheterodon madagascariensis	(CAS 54656 [633])
Liophis godmani	(CAS 67025 [628])
Lycodon aulicus	(CAS 15792 [582])
Lycodon aulicus	(CAS 15249 [278])
Lycophidion capense	(CAS 97517 [599])
Lytorhynchus ridgwayi	(CAS 101407 [596])
Macrocalamus lateralis	(CAS 94371 [630])
Masticophis flagellatum	(SU 20987 [494])
Mimophis mahfahlensis	(CAS 55122 [593])
Natrix natrix	(SU 22416 [428])
Natrix piscator	(CAS 18979 [615])
Natrix sipedon	(CAS 65048 [613])
Neusterophis olivaceous	(CAS 16964 [617])
Ninia psephota	(CAS 78869 [619])
Oligodon modestus	(SU 18887 [420])
Oxybelis aeneus	(SU 24012 [547])
Oxyrhabdium modestum	(SU 23438 [543])
Oxyrhopus fitzingeri	(CAS 14556 [632])
Pareas mollendorfi	(CAS 14949 [666])
Pareas carinatus	(CAS 73696 [644])
Philodryas elegans	(CAS 14561 [627])
Philothamnus species	(MVZ 75745)[7]
Phimophis guianensis	(CAS 94634 [614])
Phyllorhynchus decurtatus	(SU 18849 [421])

[7] Museum of Vertebrate Zoology, University of California, Berkeley, catalogue number.

Table I. *Continued.*

III. Colubridae (continued)	
Phyllorhynchus decurtatus	(CAS [538])
Pituophis catenifer	(CAS [291])
Pliocercus elapoides	(CAS 66911 [562])
Psammodynastes pulverulentes	(SU 19367 [415])
Psammophis shokeri	(CAS [393])
Psammophis shokeri	(CAS [394])
Pseudorabdion oxycephalum	(SU 18218 [423])
Ptyas korros	(CAS 19013 [580])
Rhabdophis tigrina	(CAS [631])
Rhadinea decorata	(CAS 74347 [645])
Rhinocheilus lecontei	(SU 19802 [540])
Salvadora hexalepis	(SU 21599 [493])
Sibon nebulatus	(CAS 98547 [649])
Sibynomorphus turgidus	(CAS 94295 [653])
Sibynophis collaris	(CAS 18994 [603])
Sonora semiannulata	(CAS 81402 [563])
Spalerosophis (Coluber) arenarius	(CAS [387])
Stegonotus modestus	(CAS 99918 [591])
Stilosoma extenuatum	(SU 8242 [542])
Storeria dekayi	(CAS 73964 [592])
Tachymenis chilensis	(CAS 85232 [641])
Tantilla nigriceps	(CAS 33886 [610])
Thamnophis elegans	(CAS [732–748])
Thamnophis sirtalis	(CAS 12915 [272])
Thelotornis kirtlandi	(CAS 16980 [577])
Trachischium fuscum	(CAS 38741 [588])
Trimerorhinus (Psammophylax) *rhombeatus*	(CAS 38736 [657])
Trimorphodon lyrophanes	(CAS 80656 [637])
Xenalaphis hexagonotus	(CAS 33055 [648])
Xenodon merremi	(CAS 49321 [647])
Xylophis perrottii	(CAS 17190 [651])
Zaocys dhumnades	(CAS 14651 [643])
IV. Viperidae	
Ancistrodon contortrix	(CAS 71630 [274])
Ancistrodon halys	(CAS 31512 [567])
Atheris nitschei	(CAS 85298 [559])
Atractaspis bibroni	(CAS 85812 [565])
Bitis arietans	(CAS 55109 [443])
Bothrops atrox	(CAS 71744 [276])
Causus rhombeatus	(CAS 38733 [552])
Cerastes cerastes	(CAS 84527 [568])
Crotalus atrox	(CAS 17536 [262])
Crotalus cerastes	(CAS 63090 [404])
Crotalus inyo	(CAS 90506 [407])
Crotalus viridis	(CAS [554])
Echis carinatus	(CAS 99812 [396])

TABLE I. *Continued.*

IV. Viperidae (continued)

Echis carinatus	(CAS [401])
Eristocophis mcmahoni	(CAS 99901 [573])
Sistrurus catenatus	(CAS 77793 [557])
Trimeresurus gramineus	(CAS 18737 [275])
Vipera aspis	(CAS 55150 [277])

V. Elapidae

Acanthophis antarcticus	(CAS 77793 [555])
Aspidomorphus (Brachysoma) diadema	(CAS 84067 [405])
Brachyurophis australis	(AM R3623 [725])
Bungarus multicinctus	(CAS 18881 [553])
Calliophis calligaster	(CAS 61139 [569])
Demansia psammophis	(CAS 77725 [550])
Demansia textilis	(CAS 74316 [640])
Dendroaspis sp.	(CAS 100051 [665])
Denisonia carpenteriae	(CAS 77729 [548])
Denisonia carpenteriae	(CAS 77732 [549])
Denisonia nigricens	(CAS 84052 [663])
Furina (Vermicella) annulata	(CAS 77766 [585])
Maticora bivirgata	(CAS 16778 [664])
Maticora intestinalis	(CAS 62145 [566])
Micruroides euryxanthus	(CAS 85308 [578])
Micrurus fulvius	(CAS 13136 [260])
Micrurus fulvius	(CAS 71523 [570])
Naja melanoleuca	(CAS 16981 [406])
Naja naja	(CAS 15337 [400])
Naja nigricollis	(CAS 85785 [409])
Notechis scutatus	(CAS 84047 [660])
Ophiophagus hannah	(CAS 16785 [574])
Pseudapistocalamus nymani	(CAS 99916 [583])
Pseudechis porphyriacus	(CAS 44127 [581])
Rhynchoelaps bertholdi	(AM R3103 [724])
Walterinnesia aegypti	(CAS 86378 [572])

VI. Hydrophiidae

Aipysurus eudouxi	(CAS 16857 [556])
Enhydrina shistosa	(CAS 98034 [659])
Hydrophis melanocephalus	(CAS 18850 [261])
Laticauda colubrina	(CAS 61304 [399])
Microcephalophis species	(CAS 99978 [558])
Pelamydrus platyurus	(CAS 85203 [575])
Lapemis hardwicki	(CAS 15156 [652])

The skin was not cut ventrally so that the specimen retained its value as a taxonomic specimen. 2) The muscles attaching to the otic capsule and the quadrate bone were then cut away from these bony structures. 3) The quadrate bone was severed at its superior attachment to the supratemporal bone and then

disarticulated from the lower jaw. 4) The supratemporal bone was dissected off the supralateral aspect of the otic capsule. The size and shape of the stapes could then be observed.

The prootic and opisthotic bones form an overgrowth of variable dimensions around the stapes footplate. The rim or edge of this encircling overgrowth is termed the circumfenestral crest. The degree of overgrowth of the circumfenestral crest was carefully noted as this character varied both with taxonomic status and habitat. These and all other important anatomical characters are described and figured in the text.

If the specimen was small and the otic bones thin, the point of a number 11 Bard-Parker blade was used to pick away the lateral portions of the pro- and opisthotic bones covering the sacculus. In a large specimen with thick bones, a dental drill was employed to expose the sacculus. The more ventral portions of the pro- and opisthotic bones were then removed and the edges of the circumfenestral crest widened to expose fully the stapes footplate. The size of the juxtastapedial sinus and fossa as well as the stapes footplate could then be seen. The stapes was freed from its ligamentous attachments and removed. The quadrate, supratemporal, and stapes bones were all preserved for future study.

The sacculus and utriculus were teased laterally and the acoustic nerve exposed. Both the anterior and posterior branches of the acoustic nerve were then cut and the utriculus, sacculus, and cochlear duct teased free from the vestibule and cochlear recess. In this process the peripheral portions of the semicircular ducts were destroyed, but all other portions of the labyrinth were retrieved in good shape. The sacculus together with the cochlear duct was then stored in 70 percent ethyl alcohol for detailed study. Stereophotographs were taken during the course of many dissections to serve as memoranda for future anatomical descriptions.

In addition to the collection of gross anatomical specimens, serial sections of the heads of several different snake species and sections of isolated cochlear ducts were prepared. In these cases only freshly sacrificed animals were used. Heads were fixed in neutral 10 percent formalin, decalcified, celloidin embedded, and sectioned in transverse, sagittal, and frontal planes. Cochlear ducts removed from fresh material were fixed in a variety of ways, either celloidin or parafin embedded, and stained with Hematoxylin and Eosin or Iron Hematoxylin and Aniline Blue procedures.

Detailed studies of the cochlear duct were made by carefully dissecting away the vestibular membrane to expose the limbus and papilla basilaris. The areas of both the limbic and lagenar portions of the cochlear ducts, and the papilla basilaris were determined by use of a Leitz planimeter.

To determine the degree of variation of the various portions of the cochlear duct within one species of snake, as well as to determine the changes in duct

dimensions with changes in body size and weight, the cochlear ducts were removed from 19 specimens of *Thamnophis elegans* which ranged from newborn to fully mature, and several specimens each of *Acrochordus granulatus, Psammophis shokeri, Lycodon aulicus, Herpeton tentaculatum, Constrictor constrictor, Denisonia carpenteriae, Eryx johni,* and *Typhlops proximus, T. australis,* and *T. nigricens.*

In marked contrast to the lizard cochlear duct (Miller, 1966a), where there is but minimal quantitative variation in the parts of the cochlear duct within one species, all snakes studied showed considerable variability. In all the above listed species of snakes, the degree of variation in both the limbic and lagenar area, and in the papilla basilaris length and area was approximately 25 percent. In the 19 specimens of *Thamnophis elegans* which ranged in age from newborn to large adults, the effect of age or growth on the size of the duct was of the order of 10 percent, *i.e.,* in newborn specimens the dimensions of the cochlear duct structures averaged 10 percent less than in adults, but in either newborn or adults, the range of variation is of the order of 25 percent.

To determine the effect of fixation on cochlear duct components, we studied nine fresh specimens of *Coluber florulentus.* Even in freshly removed and unfixed ducts there was an approximate 25 percent variation in the dimensions of its various parts.

If it were felt that a statistical study of the dimensions of various portions of the cochlear duct would contribute significantly to either taxonomic or acoustic problems this would have been done. However, as this was an initial survey of the structure of the snake cochlear duct, and as more than 200 species of snakes were studied, only minimal and not statistically analyzed quantitative data is given.

Even with a 25 percent variability in duct structure dimensions, however, the quantitative data presented in tables II to XII aids in showing the general size and range of cochlear duct dimensions in various snake species.

All specimens and anatomical parts are on permanent deposit in the collections of the Department of Herpetology of the California Academy of Sciences.

OBSERVATIONS

General Anatomy of the Snake Auditory Apparatus

As is well known, snakes do not have a tympanic membrane (an external ear), or a middle ear.

Sound energy is transmitted to the inner ear by bone conduction, or by means of the quadrate-stapes unit. A cartilaginous extracolumellar portion of the stapes is either attached to or articulates with the medial surface of the quadrate. In terrestrial or arboreal snakes, when the lower jaw is in resting position, the quadrate is usually acutely angulated with the ventral mandibular articulation
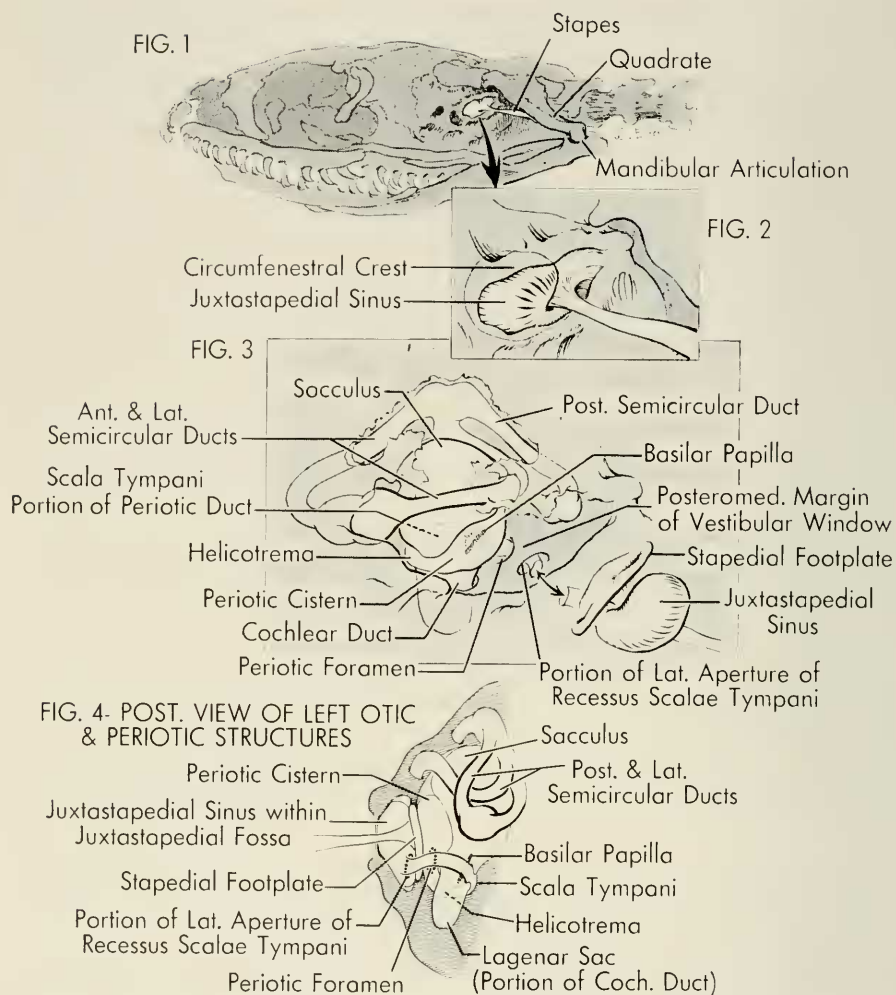
FIG. 1

Stapes

Quadrate

Mandibular Articulation

FIG. 2

Circumfenestral Crest

Juxtastapedial Sinus

FIG. 3

Sacculus

Post. Semicircular Duct

Ant. & Lat. Semicircular Ducts

Basilar Papilla

Scala Tympani Portion of Periotic Duct

Posteromed. Margin of Vestibular Window

Helicotrema

Stapedial Footplate

Periotic Cistern

Juxtastapedial Sinus

Cochlear Duct

Periotic Foramen

Portion of Lat. Aperture of Recessus Scalae Tympani

FIG. 4- POST. VIEW OF LEFT OTIC & PERIOTIC STRUCTURES

Sacculus

Post. & Lat. Semicircular Ducts

Periotic Cistern

Juxtastapedial Sinus within Juxtastapedial Fossa

Basilar Papilla

Stapedial Footplate

Scala Tympani

Portion of Lat. Aperture of Recessus Scalae Tympani

Helicotrema

Lagenar Sac (Portion of Coch. Duct)

Periotic Foramen

FIGURE 1. Left lateral view of the skull of a natricine snake to show quadrate and stapes relationships. Semidiagrammatic.

FIGURE 2. Left lateral view of stapes, circumfenestral crest, and juxtastapedial sinus. Semidiagrammatic.

FIGURE 3. Left lateral view of temporal region of skull. Portions of the prootic and opisthotic bones have been removed to show the underlying otic and periotic structures. Semidiagrammatic.

FIGURE 4. Posterior view of left otic and periotic structures. Semidiagrammatic.

FIG. 5 LAT. ASPECT OF LEFT MEMBRANOUS LABYRINTH
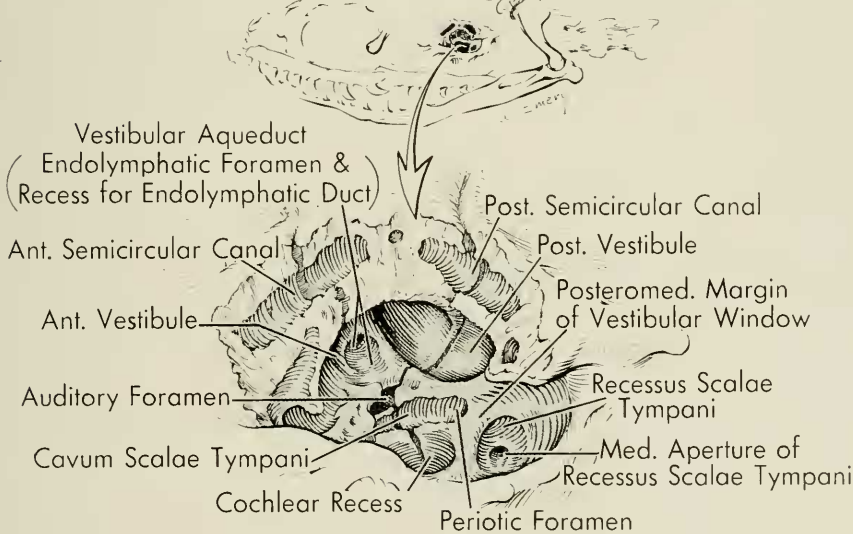(Below is Periotic System pulled away from The Cochlear Duct)

Sacculus — Crus Commune

Ant. Utricular Sinus

Ampullae of Lat. & Ant.
Semicircular Ducts

Ampulla of Post.
Semicircular Ducts

Reunient Duct
(Sacculo-Cochlear Duct)

Basilar Membrane

Basilar Papilla

Neural Limbus

Site of Adherence of Sacculus
& Cochlear Duct

Periotic Cistern

Scala Tympani

Groove for Helicotrema

Periotic Sac within
Recessus Scalae Tympani

Lagenar Sac

Helicotrema

Stapedial Footplate   Juxtastapedial Sinus

FIG. 6- MED. WALL LEFT OTIC CAVITY

Vestibular Aqueduct
Endolymphatic Foramen &
Recess for Endolymphatic Duct

Post. Semicircular Canal

Ant. Semicircular Canal

Post. Vestibule

Posteromed. Margin
of Vestibular Window

Ant. Vestibule

Auditory Foramen

Recessus Scalae
Tympani

Cavum Scalae Tympani

Med. Aperture of
Recessus Scalae Tympani

Cochlear Recess

Periotic Foramen

Figure 5. Lateral aspect of left membranous labyrinth. Semidiagrammatic.
Figure 6. Medial wall of the left otic cavity.

considerably caudal to the supratemporal attachment (fig. 1). In these species, the extracolumella-stapes is longer, and a protuberance is often present on the medial side of the quadrate where it articulates with the extracolumella. In many cases a diarthrodial joint is formed.

In burrowing and some aquatic species, the quadrate is less acutely angulated and the extracolumella-stapes is quite short. In no case is the stapes absent.

In snakes, the oval (vestibular) window, instead of facing laterally as it does in lizards, has shifted direction and faces caudally or caudolaterally (fig. 1). The stapes, thus, courses caudocephalically in snakes, rather than lateromedially as in lizards.

The vestibular foramen and the stapes footplate, which is inserted in it, and the proximal portion of the stapes may be either partially or almost completely surrounded by overgrowths of the pro- and opisthotic bones (fig. 2). This overgrown bony edge or rim is termed the circumfenestral crest. The degree of overgrowth of the circumfenestral crest is related in some degree to habitat modification, and in some degree to taxonomic groupings. Details concerning these modifications will be described under family headings.

Before describing the structures of the internal ear a clarification of terminology is in order. In this paper I have accepted the terminology used by Baird (1960) and Hamilton (1964). Thus, the membranous labyrinth proper is the otic labyrinth and the perilymphatic spaces are now termed the periotic spaces. The connection between the periotic (perilymphatic) cistern and the scala tympani portion of the periotic system is the helicotrema (formerly the perilymphatic duct). Other terms are the same as those now used by Baird (1960).

In figure 2, the structure labelled "juxtastapedial sinus" is seen situated lateral to the anterolateral portion of the stapes footplate and in part obscures it. The juxtastapedial sinus is an extracapsular extension of the periotic (perilymphatic) space, and in snakes it always covers part of the lateral aspect of the stapes footplate. The juxtastapedial sinus is confluent with the scala tympani portion of the intracapsular portion of the periotic space through a canal on the medial wall of the opisthotic bone—the interior opening of this canal is the periotic (perilymphatic) foramen, and the external opening is a portion of the lateral aperture of the recessus scalae tympani. These structures and their relationships are shown in figures 2, 3, and 4. The cavity containing the juxtastapedial sinus is the juxtastapedial fossa (fig. 4).

The portion of the lateral aperture of the recessus scalae tympani where the juxtastapedial sinus is confluent with the recessus scalae tympani portion of the periotic space is analogous to the round window of mammals (fig. 3). In lizards the periotic sac never projects beyond the lateral aperture of the recessus. In turtles there is a fluid filled space lateral to the stapes footplate. This space, the pericapsular sinus, is contiguous with, but not confluent with, the intracap-

sular periotic space. The point at which the pericapsular sinus abuts against the recessus is situated near the lateral aperture of the recessus scalae tympani.

The membranous labyrinth of snakes, as in other amniotes, is composed of three semicircular canals, a utriculus, a sacculus, and a cochlear duct (fig. 5). The cochlear duct is a posteroinferior invagination of the sacculus and in snakes is a sac-like structure housed in an inferior portion of the otic cavity, the cochlear recess. The sacculus of most snakes is smaller than in lizards and the reunient (sacculo-cochlear) duct originates approximately mid-dorsally from the posterior saccular wall (fig. 24). The more dorsal origin of the reunient duct from the sacculus is found in *Sphenodon*, a few lizards, and most snakes, and is considered a primitive feature by Hamilton (1964).

The cochlear duct of snakes is a sac-like structure composed of two distinct portions, the limbic and the lagenar (figs. 9–30). One of the most important differences between the cochlear duct of lizards and snakes is that in lizards the limbic and lagenar portions tend to be fused to form a unitary organ; in snakes the limbus and lagena are almost always constricted one from the other (figs. 38 and 39).

The limbic portion of the duct is directly connected at its dorsal pole by the reunient duct to the sacculus; it lies ventral to the sacculus and forms the dorsal portion of the cochlear duct. The lagenar sac is attached to the ventral pole of the limbus. The size of the opening between the limbus and lagena is variable, but the site of the connection is always evident as this is the point where the two parts of the cochlear duct are conjoined.

The limbic portion of the cochlear duct is a rounded-oval to elongated-oval tube. The medial wall of this tube or cylinder is formed by a peripheral ring (limbus) of dense periotic connective tissue. Enclosed by the peripheral ring or limbus is a central hiatus across which is stretched the basilar membrane upon which rests the papilla basilaris. In most lizards, the papilla is supported by a bar of periotic connective tissue which separates it from the basilar membrane (Miller, 1966a). A papillary bar has not been observed in the snake cochlear duct (figs. 7 and 8).

The acoustic branches of the auditory nerve course under the medial surface of the cephalic half of the limbic ring and ultimately supply the hair cells of the papilla basilaris (figs. 7, 13 and 14). The cephalic part of the limbic ring is, thus, referred to as the neural limbus. In most reptiles the caudal or non-neural portion of the limbus is termed the triangular limbus because of its shape in cross section.

One of the most striking characteristics of the snake limbus is that in no case (in over 200 genera) is there ever specialization of the lateral face of the neural limbus. From the entire cephalic (anterior) edge of the neural limbus a thin limbic rim projects laterally and slightly caudally. It forms a smooth walled
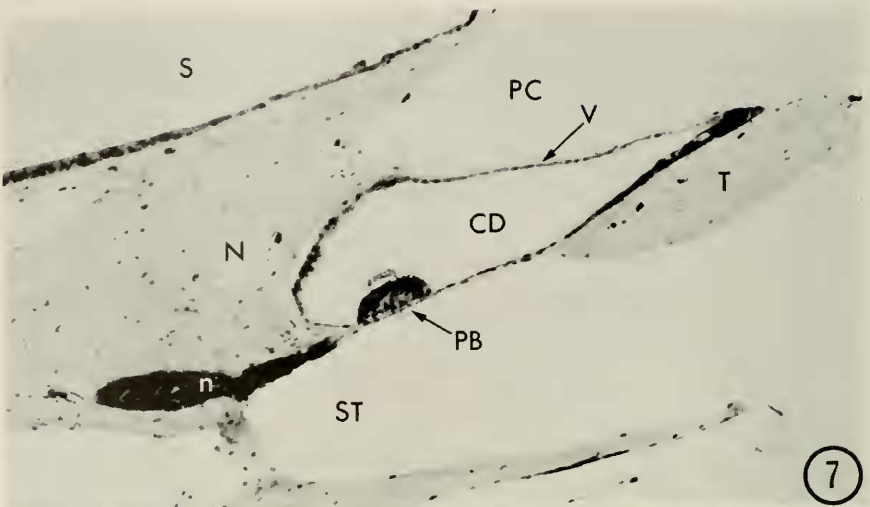
concavity on the inner (luminal) surface of the duct (figs. 7, 8 and 9). In lizards, the lateral face (luminal surface) of the neural limbus is variously modified and is different in each lizard family (fig. 38), but in all snakes is uniformly smooth and featureless. From the lateral projection of the neural limbus the vestibular or Reissner's membrane arises and forms the lateral wall of the pars limbus; it then attaches to the caudal edge of the triangular limbus.

The tectorial membrane (fig. 8) arises from the epithelial cells lining the luminal surface of the neural limbus and projects out over the papilla basilaris.

A peculiarity of snakes (and turtles) but not lizards, is that an inferior portion of the sacculus is fused to the anterior face of the pars limbus (fig. 7). This fusion is not firm as the cochlear duct may be easily separated from the sacculus by simple teasing apart of the structures.

The medial face of the limbus is slightly modified to receive the scala tympani portion of the periotic space (figs. 7, 8, and 14). As the helicotrema (figs. 5 and 10), the connection between the vestibular cistern and the scala tympani, swings out anterodorsally around the top of the lagena it enlarges into the scala tympani which abuts on the medial face of the basilar membrane and limbus. As is shown in figures 14 and 37, connective tissue extensions from the medial side of the limbus form small recesses for the scala tympani, but these are not as large nor as variable as occurs in lizards. It seems that in ducts with more elongate limbi there are both short dorsal and ventral enclosures, but in those with more rounded or ovoid shaped limbi the entire limbic face is open.

. The pars lagena (figs. 8–37) is a rounded to almost square shaped sac and forms the interior portion of the cochlear duct. The limbic lumen usually opens into the dorsolateral portion of the lagena. The vestibular membrane becomes confluent with the lateral lagenar wall. The medial wall of the lagena is formed by periotic connective tissue similar to but thinner than that of the limbus (fig. 8). an arc-like band of specialized sensory cells almost encircles the mid portion of the lagena (figs. 8 and 14). This band of cells, the macula lagenae, forms nearly three-fourths of a circle and is only deficient laterally where the

←

FIGURE 7. Cross section of cochlear duct of *Eryx johni*. This section includes a small portion of the sacculus (S) and the neural (N) and triangular (T) portions of the cochlear duct limbus. Separating the cochlear duct (CD) lumen from the periotic cistern (PC) is the vestibular membrane (V) or Reissner's membrane. An acoustic branch of the auditory nerve (n) is seen to the left of the papilla basilaris (PB). The scala tympani (ST) portion of the periotic space is medial to the papilla basilaris. The lagena is not included in this section. × 120.

FIGURE 8. Cross section of the cochlear duct of *Natrix* species. This is a section through both the limbic and lagenar portions of the cochlear duct. In addition to the structures indicated above, the macula lagenae (ML) is seen on the medial wall of the pars lagena (PL). (tm) is an oblique cut through the tectorial membrane and in the upper left part of the photograph is the spiral ganglion (SG). × 100.

pars limbus and lagena are joined. The macula lagenae is overlain by a calcareous otolithic membrane (figs. 29–30).

The differences in shape and dimensions of the pars limbi and lagenae will be discussed in detail under family headings.

Lying immediately lateral to the limbic portion of the cochlear duct is that portion of the periotic space termed the periotic (or perilymphatic) cistern (figs. 3, 4, 5, 7, and 8). In figure 5 it is drawn as though it were an enclosed and separate sac. This is not the case, however, as the periotic cistern is usually continuous dorsally with the periotic space surrounding the sacculus. Thus, in reptiles the scala vestibuli is not clearly defined as it is in mammals. Again, as seen in figures 3, 5, and 10, the periotic cistern connects by means of the anterior lagena-encircling-channel (helicotrema) to the scala tympani located directly medial to the basilar membrane. The periotic sac then continues through the periotic (perilymphatic foramen) foramen (figs. 3 and 6) into the recessus scalae tympani, and thence by the lateral aperture of the recessus to terminate extracapsularly as the juxtastapedial sinus (figs. 3, 4, 5, and 6).

Cochlear Duct Anatomy in Different Snake Families

Unlike the lizard cochlear duct, that of snakes does not provide obvious and readily discernible taxonomic clues. Therefore, I will describe and discuss the cochlear duct of snakes in relation to a rather generalized and classical taxonomic scheme.

Primitive Snake Families.

Typhlopidae	Xenopeltidae
Leptotyphlopidae	Loxocemidae
Aniliidae	Uropeltidae

Typhlopidae and Leptotyphlopidae (figs. 12 and 31):

In several very significant characteristics the anatomy of the auditory apparatus of members of these families is strictly ophidian. Even though the quadrate bone is considerably more caudal in position at its dorsal attachment than at the ventral, which is unusual in snakes, the stapes still courses cephalically from its articulation with the quadrate. This type of stapes relationship is found only in snakes. The stapes footplate is very large, flattened, thin, caudolaterally oriented, and in every way like that of other burrowing snakes. Of greatest significance is that in large species such as *Typhlops nigrescens* and *T. proximus* there is a juxtastapedial sinus situated lateral to the stapes footplate. To my knowledge, the development of a juxtastapedial sinus is a purely ophidian innovation.

In addition to the above extracapsular anatomical features, the cochlear duct of all species of *Liotyphlops*, *Typhlops*, and *Leptotyphlops* examined is

TABLE II.[8]   *Papilla basilaris length and area and limbic/lagenar ratio in the Typhlopidae and Leptotyphlopidae.*

Length of papilla basilaris (mm.)			Area of papilla basilaris (mm.²)			Ratio $\frac{Area\ limbus}{Area\ lagena}$		
1. *Typhlops bituber-*			1. *T. bitubercu-*			1. *T. bituber-*		
culatus	722	.12	latus	722	.006	culatus	722	.60
2. *Typhlops bituber-*			2. *T. bitubercu-*			2. *T. nigrescens*	718	.63
culatus	721	.14	latus	721	.008			
3. *Typhlops nigrescens*	718	.16	3. *T. australis*	719	.015	3. *T. bituber-*		
						culatus	721	.67
4. *Typhlops australis*	720	.23	4. *T. australis*	720	.019	4. *T. australis*	719	.68
5. *Typhlops australis*	719	.24	5. *T. proximus*	716	.019	5. *T. proximus*	714	.71
6. *Typhlops proximus*	716	.28	6. *T. nigrescens*	718	.023	6. *T. proximus*	715	.79
7. *Typhlops proximus*	714	.29	7. *T. proximus*	714	.023	7. *T. proximus*	716	.80
8. *Typhlops proximus*	715	.30	8. *T. proximus*	715	.024	8. *T. australis*	720	.85

[8] In Tables II to VIII the species designations have been omitted from the second and third columns except in cases where more than one species of a genus are represented.

typically ophidian and is in no way similar to that of any other type of reptile (compare figs. 12 and 31 with 38 and 39).

The limbus and papilla basilaris of most species studied was ovoid-elongate but there was greater limbic elongation in *T. lumbricalis* and *T. nigrescens*. Considering that all species of these two snake families are burrowers, it was somewhat surprising that the limbi were not of the elongate type as is true in most other snake families where there is a rather close correlation between limbic elongation and burrowing habitus. In comparing the relative degree of papillar elongation in species of these families with those of other primitive families (fig. 31, tables II and III), it will be observed that the situation in the Typhlopidae and Leptotyphlopidae is one of but moderate elongation. It is possible that the great diminution in general skull size in these snakes has had some influence on the size of membranous labyrinth components.

If one compares the cochlear duct of other small burrowing reptiles, such as that of *Dibamus* or *Anelytropsis* or an amphisbaenid, with that of a typhlopid or leptotyphlopid (compare figs. 12 and 31 with 38 and 39) the following similarities and differences are apparent: 1) the limbi of *Dibamus* and *Anelytropsis* as well as those of typhlopids and leptotyphlopids have no lips, but the fact that the limbi and lagenae are joined in *Dibamus* and *Anelytropsis* but not joined in typhlopids and leptotyphlopids characterize the former as lizard and the latter as snake types; 2) the cochlear duct of amphisbaenids have both limbic lips and the parts conjoined; they are, therefore, lizard-like; 3) the quadrate-stapes relationships and lack of a juxtastapedial sinus in *Dibamus*, *Anelytropsis*, and the amphisbaenids also affirm their lacertilian affinities as does the anatomy of this region confirm the ophidian nature of the typhlopids and leptotyphlopids.
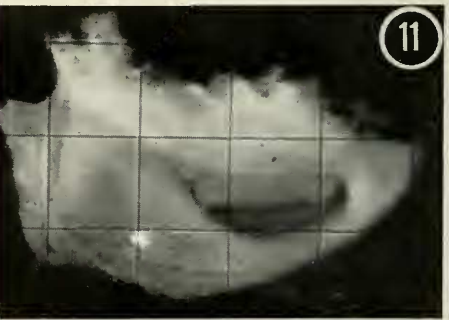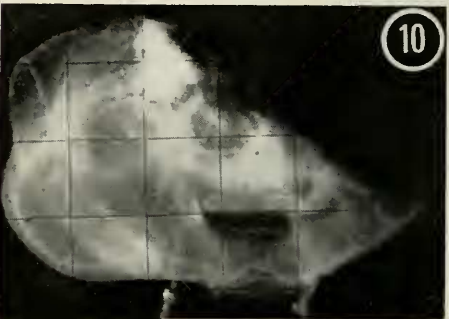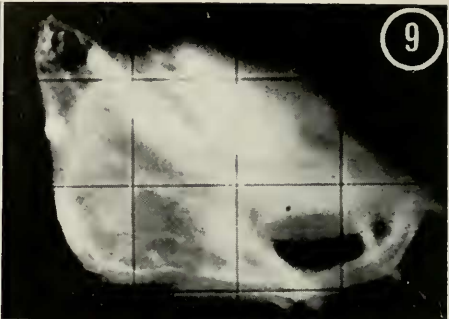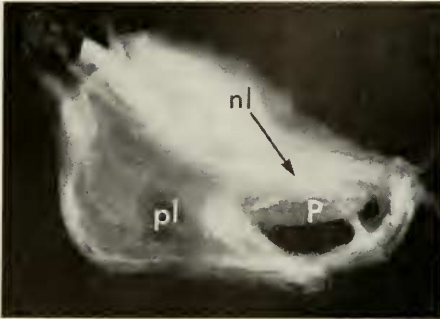
TABLE III. *Papilla basilaris length and area and limbic/lagenar ratio in the primitive families Aniliidae, Loxocemidae, Xenopeltidae, and Uropeltidae.*

Length of papilla basilaris (mm.)		Area of papilla basilaris (mm.²)		Ratio $\dfrac{Area\ limbus}{Area\ lagena}$	
1. *Rhinophis oxyrhynchus*	.24	1. *Rhinophis*	.016	1. *Anilius*	.72
2. *Plectrurus aureus*	.31	2. *Platypectrurus*	.025	2. *Rhinophis*	1.1
3. *Anilius scytale*	.40	3. *Plectrurus*	.027	3. *Loxocemus*	1.3
4. *Platypectrurus*		4. *Anilius*	.029	4. *Xenopeltis*	1.4
madurensis	.40				
5. *Cylindrophis rufus*	.53	5. *Xenopeltis*	.068	5. *Cylindrophis*	1.9
6. *Loxocemus bicolor*	.64	6. *Cylindrophis*	.081	6. *Plectrurus*	2.4
7. *Xenopeltis unicolor*	.79	7. *Loxocemus*	.112	7. *Platypectrurus*	2.4

In general the cochlear duct of typhlopids and leptotyphlopids is typically ophidian and possesses no features that clearly demarcate it from that of other snakes; the duct must, by reason of its structure, be referred to the class of snake cochlear ducts that are associated with species that are burrowing.

Aniliidae, Xenopeltidae, Loxocemidae, and Uropeltidae (figs. 9, 10, 11, 12, and 31; table III).

This group of primitive snakes are all burrowing to a greater or lesser extent and as such show modifications of the quadrate, stapes, and recessus scalae tympani found in other burrowing species. The details of the anatomy of the extracapsular structures will not be presented here but will be the subject of a discourse on the modifications of the temporal region of the skull in burrowing reptiles. Suffice to state the bony temporal anatomy in these species is typically ophidian.

The essential feature of the cochlear duct in these families is an elongate limbus and papilla basilaris. This condition is characteristic of burrowing species


←

PRIMITIVE FAMILIES

FIGURE 9.[2] *Anilius scytale* (CAS [501]). The papilla basilaris (P) is moderately elongate, and the lagenar sac (pl) somewhat reduced in size; (nl) is the edge of the neural limbus. × 40.

FIGURE 10. *Loxocemus bicolor* (CAS [416]). The papilla basilaris is quite elongate and the lagenar sac is fairly large. The helicotrema (h) is intact in this photograph as it curves around the upper rim of the lagena. × 25.

FIGURE 11. *Platypectrurus madurensis* (CAS [478]). The papilla is large and elongate but the lagenar sac is very much reduced in size. × 50.

FIGURE 12. *Typhlops nigrescens* (CAS [717]). The papilla is elongate and the lagenar sac moderate in size. The exact position of the macula lagenae may be somewhat different in *Typhlops* than it is in other snakes, but this has not been adequately studied as yet. × 37.

---

[2] Figures 9 to 30, inclusive, are stereophotographs of the left cochlear ducts. Except where noted, the lateral aspect has been photographed and the dorsal portion of the duct is to the right, and the ventral is to the left.
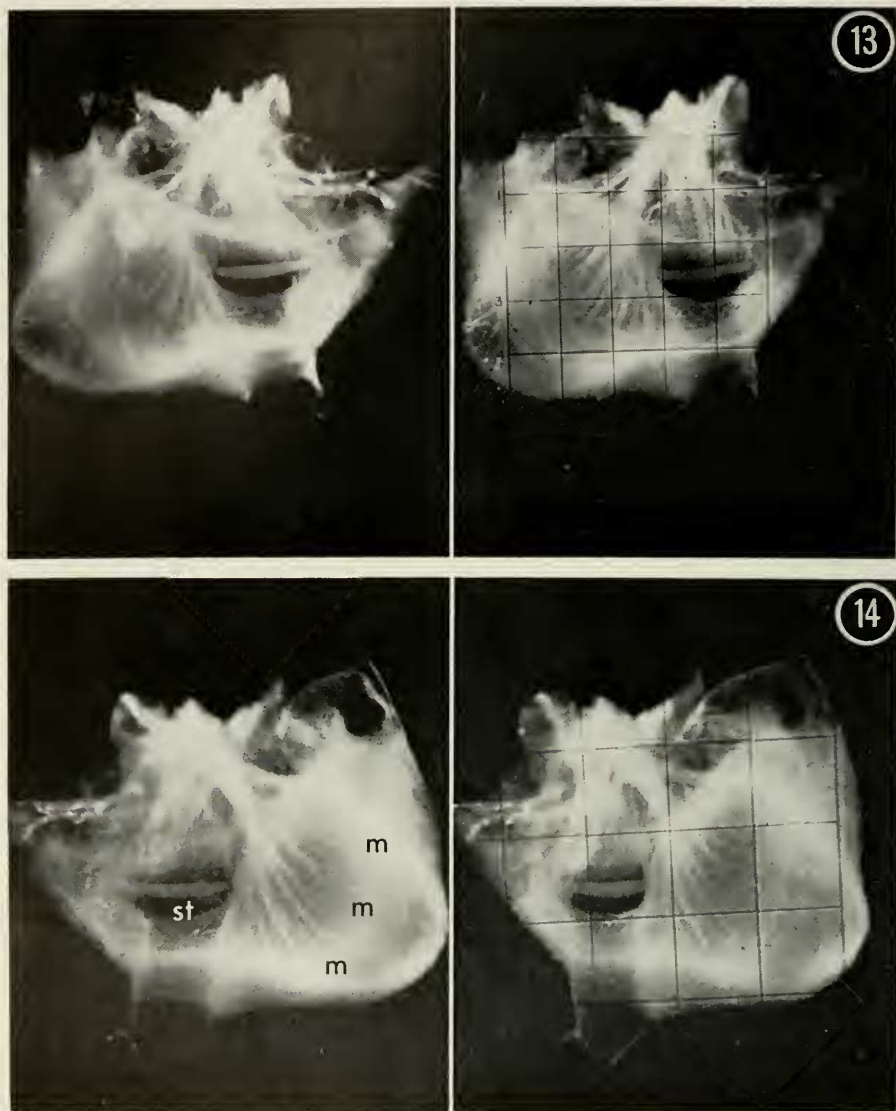
FAMILY BOIDAE
Eunectes murinus (CAS [656]).

FIGURE 13. Lateral aspect. The papilla is elongate and the lagenar sac is large. The small bundles of nerve fibers supplying the papilla basilaris are clearly seen. × 19.

FIGURE 14. Medial aspect. The nerve fibers to both the papilla and the macula lagenae are clearly visualized. The macula lagenae (m) is seen as an arclike band on the luminal wall of the lagenar sac. The helicotrema is easily followed to the scala tympani (st) portion of the periotic space lying immediately medial to the basilar membrane. An enclosed dorsal portion of the scala tympani is present. × 22.

TABLE IV. *Papilla basilaris length and area and limbic/lagenar ratio in the Boidae.*

Length of papilla basilaris (mm.)		Area of papilla basilaris (mm.²)		Ratio $\dfrac{Area\ limbus}{Area\ lagena}$	
1. *Charina bottae*	.32	1. *Epicrates*	.029	1. *Eunectes murinus*	.56
2. *Tropidophis melanurus*	.37	2. *Charina bottae*	.030	2. *Python*	.64
3. *Epicrates exsul*	.38	3. *Lichanura*	.033	3. *Charina bottae*	.64
4. *Liasis childreni*	.38	4. *Liasis*	.033	4. *Enygrus*	.68
5. *Lichanura roseofusca*	.41	5. *Tropidophis*	.035	5. *Liasis*	.73
6. *Calabaria reinhardtii*	.45	6. *Eryx conica*	.035	6. *Lichanura*	.78
7. *Enygrus carinatus*	.47	7. *Enygrus*	.040	7. *Epicrates*	.81
8. *Chondropython viridis*	.49	8. *Calabaria*	.041	8. *Tropidophis*	.82
9. *Eryx conica*	.55	9. *E. johni* [355]	.046	9. *Chondropython*	.89
10. *Constrictor constrictor* [602]	.68	10. *E. johni* [397]	.051	10. *Eryx conica*	.97
11. *Eunectes murinus*	.69	11. *Constrictor* [602]	.055	11. *Constrictor* [408]	1.02
12. *Constrictor constrictor* [408]	.73	12. *Eunectes*	.055	12. *Constrictor* [602]	1.07
13. *Eryx johni* [355]	.76	13. *Constrictor* [408]	.059	13. *Calabaria*	1.32
14. *Eryx johni* [397]	.78	14. *Python*	.078	14. *Eryx johni*	2.04
15. *Python molurus*	.86	15. *Chondropython*	.096		

in general. As a consequence of the elongation of the limbus, the lagena seems to have been reduced in size and is reduced most in uropeltids (figs. 11 and 31).

The papilla basilaris of *Anilius scytale*, while elongate, is less elongate than the other species of this group. The papillae of *Xenopeltis*, *Cylindrophis*, and *Loxocemus* are by contrast, extremely elongate. In table III the uropeltid genera *Plectrurus* and *Platypectrurus* show a high limbic lagenar ratio, but this is a reflection of the extreme lagenar reduction in the uropeltids and is not due to great development of the limbus *per se*. Of all snakes studied, the uropeltids have the greatest degree of lagenar reduction. Of further significance is the fact that, with very few exceptions, *Cylindrophis*, *Loxocemus*, and *Xenopeltis* have both the longest and largest papilla basilaris of all snakes observed.

Boidae (figs. 13, 14 and 31; table IV).

Members of this family usually have stout stapes, a moderately open or only slightly closed circumfenestral crest, a large juxtastapedial sinus, a large external recessus aperture, and a stapes which tends to join the stapes footplate excentrically on the lateral side. The bony ear region of the skull is expanded and the cochlear recess is large.

The limbus of the cochlear duct is generally elongate, even in non-burrowing forms. As in species of other families, however, the most elongate papillae basilares are found in burrowing species such as in *Calabaria reinhardti* and *Eryx johni* (fig. 31). In small burrowing species such as in *Charina bottae* and *Lichanura roseofusca* (fig. 31), the limbus is not as elongate as one might expect.
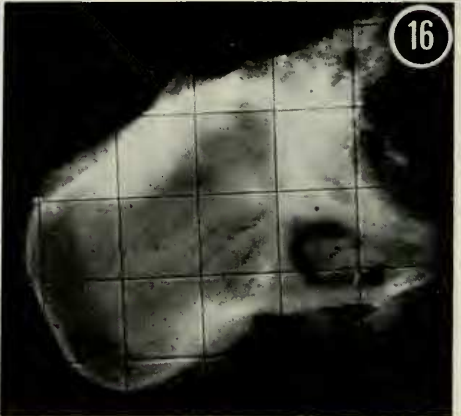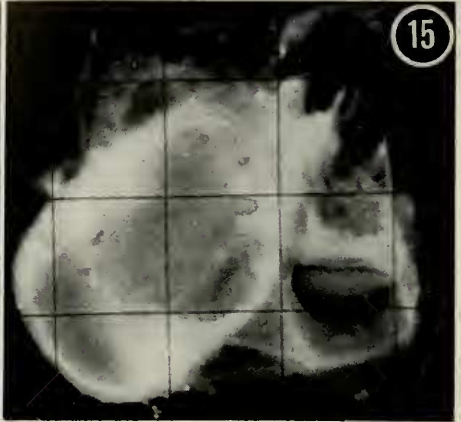
That limbic elongation is not inevitably associated with the burrowing habitus is reflected in the elongate limbi of *Constrictor constrictor, Eunectes murinus,* and *Liasis childreni* (fig. 31). It is possible that the ancestral boids were fossorial (as are most other primitive snakes) and had developed elongate limbi in the cochlear duct. The presence of elongate limbi in modern terrestrial species may signify the retention of a primitive anatomical feature.

As the area of the limbus and papilla basilaris usually is greatest in the larger species in all snake families, it is not surprising to find this true in *Constrictor, Python,* and *Chondropython* (fig. 31, table IV). Even considering body size, however, the papilla is larger in the boids than it is in most species of the more advanced families. In general, the lagenar sac is of fairly generous proportions in the boids, but it is never as enlarged as in many species of the more advanced families (compare fig. 31 with 32–35).

Whether the large size of the papilla basilaris in boids and other primitive snake families is related to better hearing capacity is unknown as no physiological studies have been reported on the acoustical abilities of these snakes.

Colubridae (figs. 15–20, 32 and 33; tables V–IX; chart 1).

As might be expected, the detailed anatomy of the bony temporal region as well as that of the cochlear duct shows considerable variation among the colubrids. In general, the anatomical details of the bony temporal region vary in accordance with the modification of the species to a particular habitat.

In wide-gaping species with long angulated quadrates, the extracolumellar-stapes unit is long and slender, while in species modified for burrowing, the quadrate is shorter, thicker, and more upright in position, and the stapes is shorter and flatter.

The circumfenestral crest varies from widely open to partially closed, but a particular situation is not clearly associated with a particular habitat modification. The juxtastapedial sinus is large, but never enormous, and in a few cases is much narrowed. The stapes footplate is fairly large; in heavy bodied

---

←

FAMILY COLUBRIDAE

FIGURE 15. *Pituophis catenifer* (CAS [291]). This is a "typical" terrestrial colubrid type cochlear duct with a more ovoid than elongate limbus, a slightly elongate papilla and a fairly large lagenar sac. × 40.

FIGURE 16. *Boiga irregularis* (CAS [560]). An arboreal colubrid in which the limbic area is probably mildly reduced in size and is considerably smaller relative to the large lagenar sac. × 42.

FIGURE 17. *Enhydris pakistanica* (CAS [402]). An aquatic colubrid in which there has been considerable absolute reduction of the papilla basilaris. As occurs in most aquatic colubrids, the lagena is very large. Note the well defined macula lagenae. The sacculus, with a torn lateral wall, remains in place. Note the posterodorsal site of origin of the sacculo-cochlear duct and the square shape of the sacculus. × 27.

TABLE V. *Papilla basilaris length and area and limbic/lagenar ratio in some terrestrial colubrids.*

Length of papilla basilaris (mm.)		Area of papilla basilaris (mm.²)		Ratio $\dfrac{Area\ limbus}{Area\ lagena}$	
1. *Crotaphopeltis hotamboeia*	.19	1. *Psammophis*	.011	1. *Coluber*	.27
2. *Psammophis shokeri*	.19	2. *Heterodon*	.012	2. *Crotaphopeltis*	.33
3. *Coluber constrictor*	.21	3. *Crotaphopeltis*	.015	3. *Zaocys*	.37
4. *Heterodon platyrhinus*	.23	4. *Coluber*	.015	4. *Masticophis*	.41
5. *Salvadora hexalepis*	.24	5. *Phimophis*	.016	5. *Heterodon*	.43
6. *Trimorphodon lyrophanes*	.24	6. *Coronella*	.019	6. *Alsophis*	.43
7. *Coronella austriaca*	.24	7. *Salvadora*	.019	7. *Salvadora*	.45
8. *Psammophylax rhombeatus*	.25	8. *Dromicus*	.020	8. *Drymarchon*	.47
9. *Dromicus hoodensis*	.27	9. *Trimorphodon*	.021	9. *Lampropeltis*	.47
10. *Leptodeira punctata*	.28	10. *Psammophylax*	.023	10. *Psammophis*	.49
11. *Phimophis guanensis*	.29	11. *Drymarchon*	.024	11. *Dryadophis*	.52
12. *Drymarchon corais*	.31	12. *Dryadophis*	.024	12. *Trimorphodon*	.52
13. *Lampropeltis getulus*	.31	13. *Leptodeira*	.025	13. *Lioheterodon*	.54
14. *Masticophis flagellatum*	.33	14. *Alsophis*	.026	14. *Psammophylax*	.54
15. *Alsophis vudii*	.33	15. *Lampropeltis*	.029	15. *Phimophis*	.55
16. *Xenodon merremi*	.35	16. *Natrix*	.031	16. *Xenodon*	.56
17. *Dryadophis melanolomus*	.35	17. *Xenodon*	.031	17. *Natrix*	.58
18. *Natrix natrix*	.40	18. *Masticophis*	.033	18. *Dromicus*	.60
19. *Lioheterodon madagascariensis*	.42	19. *Zaocys*	.035	19. *Spalerosophis*	.64
20. *Zaocys dhumnades*	.44	20. *Spalerosophis*	.045	20. *Coronella*	.64
21. *Spalerosophis arenarius*	.57	21. *Lioheterodon*	.046	21. *Leptodeira*	.84

terrestrial species it is thicker and less expanded, while in burrowers it is larger, flatter, and thinner. The recessus scalae tympani is variable in size and shape.

The cochlear duct is markedly variable in size and shape and the degree of development of its various parts is usually correlated with specific habitat modifications as is true of the bony temporal region.

A typical terrestrial colubrid (fig. 32) has an ovoid to only slightly elongate limbus and a lagenar sac area approximately twice that of the limbus. *Spalerosophis arenarius* (figs. 19 and 32), a terrestrial colubrid, has an unusually elongate papilla. As a rule larger species have larger papillae basilares.

Examination of chart 1 reveals that the cochlear duct of arboreal colubrids

←

FAMILY COLUBRIDAE

FIGURE 18. *Acrochordus granulatus* (CAS [417]). The limbus has been markedly reduced, but the papilla basilaris has remained large and elongate. An elongate papilla is unusual in an aquatic snake. The lagenar sac is large as in other aquatic snakes. × 28.

FIGURE 19. *Spalerosophis arenarius* (CAS [387]). The papilla is somewhat more elongate than is usual for terrestrial colubrid snakes. Compare with Fig. 32. × 24.

FIGURE 20. *Calamaria gervaisi* (CAS [410]). This is an example of a truly burrowing colubrid snake with a markedly elongate papilla. The lagenar sac is reduced in size. × 56.

Chart I. *Showing limbic/lagenar ratios in the Colubridae.*

$\frac{Area\ limbus}{Area\ lagena} \times 100$	Secretive-burrowing	Terrestrial	Terrestrial-arboreal	Arboreal	Aquatic
				Boiga	
					Acrochordus gran.
				Dispholidus	
		Coluber			
				Dendrelaphis	Acrochordus jav.
				Oxybelis	
30				Ahaetulla	
		Crotaphopeltis			
			Ptyas	Imantodes	
				Chrysopelea	Herpeton
	Contia				
		Zaocys		Thelatornis	
			Drymobius		
				Sibon	
					Cerberus
40		Masticophis		Helicops	Gonyosoma
		Heterodon	Lycodon		
		Alsophis	Chlorophis		
	Liodytes	Salvadora		Aplopeltura	
		Drymarchon			
		Lampropeltis			
		Psammophis			
			Elaphe		
50		Dryadophis	Psammody-		
		Trimorphodon	nastes		
		Lioheterodon			Enhydris
	Arizona	Psammophylax			
	Diadophis	Phimophis			
	Phyllorhynchus	Xenodon			
	Chilomeniscus	Natrix			
60	Storeria	Dromicus	Dasypeltis		
	Pliocercus				Fordonia
	Sibynophis	Spalerosophis			
		Coronella			
			Pareas		
			Mimophis		
			Stegonotus		
70	Chionactus				
	Abastor				
	Cemophora				
	Hypsiglena				
	Duberria				
	Ninia				

CHART I. *Continued.*

$\dfrac{Area\ limbus}{Area\ lagena} \times 100$	Secretive-burrowing	Terrestrial	Terrestrial-arboreal	Arboreal	Aquatic
80					
	Carphophis				
	Sonora				
	Rhadinia				
	Tachymenis				
	Coniophanes	*Leptodeira*			
	Sibynomorphus				
	Rhinocheilus				
	Lycophidion				
90					
	Trachischium				
	Geophis				
100					
	Farancia				
	Lytorhynchus				
	Ficimia				
	Xylophis				
	Liophis				
> 100	*Tantilla*				
	Haldea				
	Macrocalamus				
	Aparallactus				
	Calamaria				
	Pseudorabdion				

shows a reduction of the area of the limbus relative to that of the lagena, whereas in secretive-burrowing species the reverse is true. In those species that are classified as terrestrial-arboreal, the proportions of the cochlear duct parts are much as they are in the terrestrial species. The duct of *Gonyosoma oxycephalum* (fig. 32) seems unusual for a supposedly arboreal colubrid (Taylor, 1922; Smith, 1943) in that the limbus is relatively elongate, but the lagenar sac is large. Thus, the relative proportions of the pars limbi and lagenae are just as important factors in evaluating cochlear duct differences as are the differences in the shape and size of the papilla basilaris.

In aquatic colubrids (fig. 33), as in arboreal species, there is a relative reduction of the pars limbus. In *Enhydris pakistanica* and *Herpeton tentaculum*,

TABLE VI. *Papilla basilaris length and area and limbic/lagenar ratio in some terrestrial-arboreal colubrids.*

Length of papilla basilaris (mm.)		Area of papilla basilaris (mm.²)		Ratio $\frac{Area\ limbus}{Area\ lagena}$	
1. *Dasypeltis scabra*	.18	1. *Dasypeltis*	.010	1. *Ptyas*	.34
2. *Mimophis mahfahlensis*	.19	2. *Mimophis*	.016	2. *Drymobius*	.38
3. *Lycodon aulicus*	.23	3. *Lycodon*	.016	3. *Lycodon*	.43
4. *Pareas carinatus*	.25	4. *Pareas*	.018	4. *Chlorophis*	.43
5. *Chlorophis irregularis*	.26	5. *Chlorophis*	.021	5. *Elaphe*	.50
6. *Stegonotus modestus*	.31	6. *Drymobius*	.024	6. *Psammodynastes*	.51
7. *Psammodynastes pulverulentes*	.32	7. *Stegonotus*	.028	7. *Dasypeltis*	.60
8. *Drymobius margaretiferus*	.32	8. *Psammodynastes*	.029	8. *Pareas*	.68
9. *Elaphe obsoleta*	.36	9. *Elaphe*	.034	9. *Mimophis*	.68
10. *Ptyas korros*	.45	10. *Ptyas*	.065	10. *Stegonotus*	.69

TABLE VII. *Papilla basilaris length and area and limbic/lagenar ratio in some arboreal colubrids.*

Length of papilla basilaris (mm.)		Area of papilla basilaris (mm.²)		Ratio $\frac{Area\ limbus}{Area\ lagena}$	
1. *Imantodes gemmistratus*	.15	1. *Imantodes*	.011	1. *Boiga*	.23
2. *Oxybelis aeneus*	.18	2. *Oxybelis*	.011	2. *Dispholidus*	.25
3. *Chrysopelea paradesi*	.21	3. *Dispholidus*	.013	3. *Dendrelaphis*	.28
4. *Aplopeltura boa*	.21	4. *Chrysopelea*	.013	4. *Oxybelis*	.29
5. *Sibon nebulatus*	.23	5. *Ahaetulla*	.015	5. *Ahaetulla*	.31
6. *Ahaetulla prasina*	.25	6. *Aplopeltura*	.017	6. *Imantodes*	.33
7. *Boiga irregularis*	.26	7. *Sibon*	.019	7. *Chrysopelea*	.34
8. *Thelatornis kirtlandi*	.28	8. *Dendrelaphis*	.022	8. *Thelatornis*	.36
9. *Dendrelaphis caudolineatus*	.29	9. *Boiga*	.023	9. *Sibon*	.39
10. *Dispholidus typus*	.32	10. *Thelatornis*	.023	10. *Gonyosoma*	.42
11. *Gonyosoma oxycephalum*	.43	11. *Gonyosoma*	.042	11. *Aplopeltura*	.44

TABLE VIII. *Papilla basilaris length and area and limbic/lagenar ratio in some aquatic colubrids.*

Length of papilla basilaris (mm.)		Area of papilla basilaris (mm.²)		Ratio $\frac{Area\ limbus}{Area\ lagena}$	
1. *Enhydris pakistanica*	.11	1. *Enhydris*	.006	1. *Acrochordus granulatus*	.24
2. *Herpeton tentaculatum*	.14	2. *Herpeton*	.009	2. *Acrochordus javanicus*	.28
3. *Helicops angulatus*	.24	3. *Helicops*	.018	3. *Herpeton*	.34
4. *Cerberus rhynchops*	.35	4. *Cerberus*	.026	4. *Cerberus*	.40
5. *Fordonia leucobalia*	.45	5. *Fordonia*	.032	5. *Helicops*	.40
6. *Acrochordus granulatus*	.47	6. *Acrochordus granulatus*	.040	6. *Enhydris*	.53
7. *Acrochordus javanicus*	1.5	7. *Acrochordus javanicus*	.140	7. *Fordonia*	.64

TABLE IX. *Papilla basilaris length and area and limbic/lagenar ratio in some secretive-burrowing colubrids.*

Length of papilla basilaris (mm.)		Area of papilla basilaris (mm.²)		Ratio $\dfrac{Area\ limbus}{Area\ lagena}$	
1. *Duberria lutrix*	.14	1. *Storeria*	.006	1. *Contia*	.36
2. *Contia tenuis*	.15	2. *Duberria*	.008	2. *Liodytes*	.45
3. *Sonora semiannulata*	.15	3. *Sonora*	.009	3. *Arizona*	.57
4. *Storeria dekayi*	.15	4. *Contia*	.011	4. *Diadophis*	.58
5. *Diadophis amabilis*	.18	5. *Ninia*	.011	5. *Phyllorhynchus*	.58
6. *Chionactis occipitalis*	.18	6. *Carphophis*	.012	6. *Chilomeniscus*	.60
7. *Carphophis amoenus*	.20	7. *Diadophis*	.012	7. *Storeria*	.60
8. *Ninia psephota*	.21	8. *Hypsiglena*	.014	8. *Pliocercus*	.60
9. *Tantilla nigriceps*	.22	9. *Trachischium*	.014	9. *Sibynophis*	.61
10. *Haldea striatulata*	.22	10. *Tachymenis*	.014	10. *Chionactis*	.70
11. *Chilomeniscus cinctus*	.23	11. *Tantilla*	.014	11. *Abastor*	.73
12. *Lycophidion capense*	.23	12. *Haldea*	.015	12. *Cemophora*	.73
13. *Aparallactus capensis*	.23	13. *Chionactis*	.015	13. *Hypsiglena*	.77
14. *Liodytes alleni*	.24	14. *Chilomeniscus*	.015	14. *Duberria*	.78
15. *Hypsiglena torquata*	.24	15. *Lycophidion*	.016	15. *Ninia*	.78
16. *Trachischium fuscum*	.24	16. *Aparallactus*	.016	16. *Carphophis*	.80
17. *Tachymenis chilensis*	.25	17. *Geophis*	.018	17. *Sonora*	.80
18. *Geophis nasalis*	.25	18. *Liodytes*	.018	18. *Rhadinea*	.81
19. *Ficimia olivacea*	.26	19. *Sibynomorphus*	.019	19. *Tachymenis*	.82
20. *Sibynomorphus turgidus*	.27	20. *Pseudorabdion*	.019	20. *Coniophanes*	.83
21. *Rhadinia decorata*	.29	21. *Ficimia*	.019	21. *Sibynomorphus*	.88
22. *Liophis godmani*	.29	22. *Xylophis*	.021	22. *Rhinocheilus*	.88
23. *Pseudorabdion oxycephalum*	.30	23. *Rhinocheilus*	.022	23. *Lycophidion*	.89
24. *Xylophis perrottii*	.31	24. *Lytorhynchus*	.023	24. *Trachischium*	.90
25. *Rhinocheilus lecontei*	.31	25. *Rhadinia*	.023	25. *Geophis*	.93
26. *Cemophora coccinea*	.32	26. *Liophis*	.024	26. *Farancia*	1.05
27. *Abastor erythrogrammus*	.32	27. *Phyllorhynchus*	.025	27. *Lytorhynchus*	1.05
28. *Lytorhynchus ridgwayi*	.32	28. *Cemophora*	.026	28. *Ficimia*	1.16
29. *Pliocercus elapoides*	.34	29. *Farancia*	.027	29. *Xylophis*	1.16
30. *Phyllorhynchus decurtatus*	.34	30. *Calamaria*	.031	30. *Liophis*	1.20
31. *Sibynophis collaris*	.37	31. *Sibynophis*	.032	31. *Tantilla*	1.20
32. *Calamaria gervaisi*	.39	32. *Pliocercus*	.032	32. *Haldea*	1.25
33. *Coniophanes punctigularis*	.40	33. *Abastor*	.033	33. *Macrocalamus*	1.28
34. *Farancia abacura*	.40	34. *Macrocalamus*	.038	34. *Aparallactus*	1.56
35. *Arizona elegans*	.44	35. *Coniophanes*	.041	35. *Calamaria*	1.63
36. *Macrocalamus lateralis*	.45	36. *Arizona*	.054	36. *Pseudorabdion*	2.43

there is absolute reduction in the size of the papilla basilaris. The cochlear duct of *Acrochordus javanicus* (fig. 33) is one of the largest I have observed in this survey. It is particularly interesting that the papilla basilaris is large and long despite the fact that the stapes is small, and the juxtastapedial sinus and fossa are much reduced. Also, the very large size of the lagenar sac in *Acrochordus* as well as in other aquatic colubrids and in the hydrophiids evokes speculation

concerning the possible function of the macula lagenae in the ear of aquatic reptiles.

An important consideration that must not be overlooked is that in burrowing species the skull becomes heavier and more compressed; thus, there may be less space available to accommodate the cochlear duct part of the membranous labyrinth. In these cases the reduction of the lagena may be associated with reduced cochlear recess size, but the concomitant elongation and enlargement of the limbus and papilla indicate that there is a definite relationship between a burrowing mode of life and a larger and more well developed papilla.

The fact that the extracapsular auditory structures are also well developed in burrowing species and much reduced in aquatic species leads me to believe that auditory signals are much more significant in the life of burrowing snakes and probably little used by most aquatic snakes. However, it must be remembered that the macula lagenae may play an as yet undiscovered and significant role.

Viperidae (figs. 21–23 and 34; table X).

In viperids the juxtastapedial sinus is moderately to almost completely closed by the circumfenestral crest. The juxtastapedial sinus is moderately large and the stapes footplate fairly large, heavy, and not much flattened.

Considering the large size of many viperids, the papilla basilaris is not correspondingly large. In general aspect, the viperid cochlear duct is very similar to that of a terrestrial colubrid with a slightly elongate limbus and a lagenar sac approximately twice the size of the limbus.

Among the viperids, *Bitis arietans* (fig. 34) has a rather elongated papilla basilaris. The lagenar-limbic ratio shows that the limbus is well developed in *Atheris nitschei*, but apparently this is because of lagenar reduction, and not limbic elongation. *Atractaspis bibroni* (fig. 34), a "burrowing viperid," does not exhibit a particularly long papilla. It would seem that the pars lagena has been markedly reduced in this species which may reflect merely reduction in cochlear space coincident with decrease in skull size.

→

Family Viperidae

FIGURE 21. *Crotalus viridis* (CAS [554]). A "typical" viperid cochlear duct very similar to that of most terrestrial colubrids. The papilla is somewhat elongate and the lagena fairly large. × 54.

FIGURE 22. *Atheris nitschei* (CAS [559]). The papilla is less elongate in this species. The white line behind (medial to) the papilla is an accessory nerve branch to the posterior ampulla. The calcium laden otolithic membrane (broken in three places) is prominent within the lagenar sac. × 48.

FIGURE 23. *Ancistrodon contortrix* (CAS [274]). This duct is much like that of most terrestrial colubrid snakes. × 50.
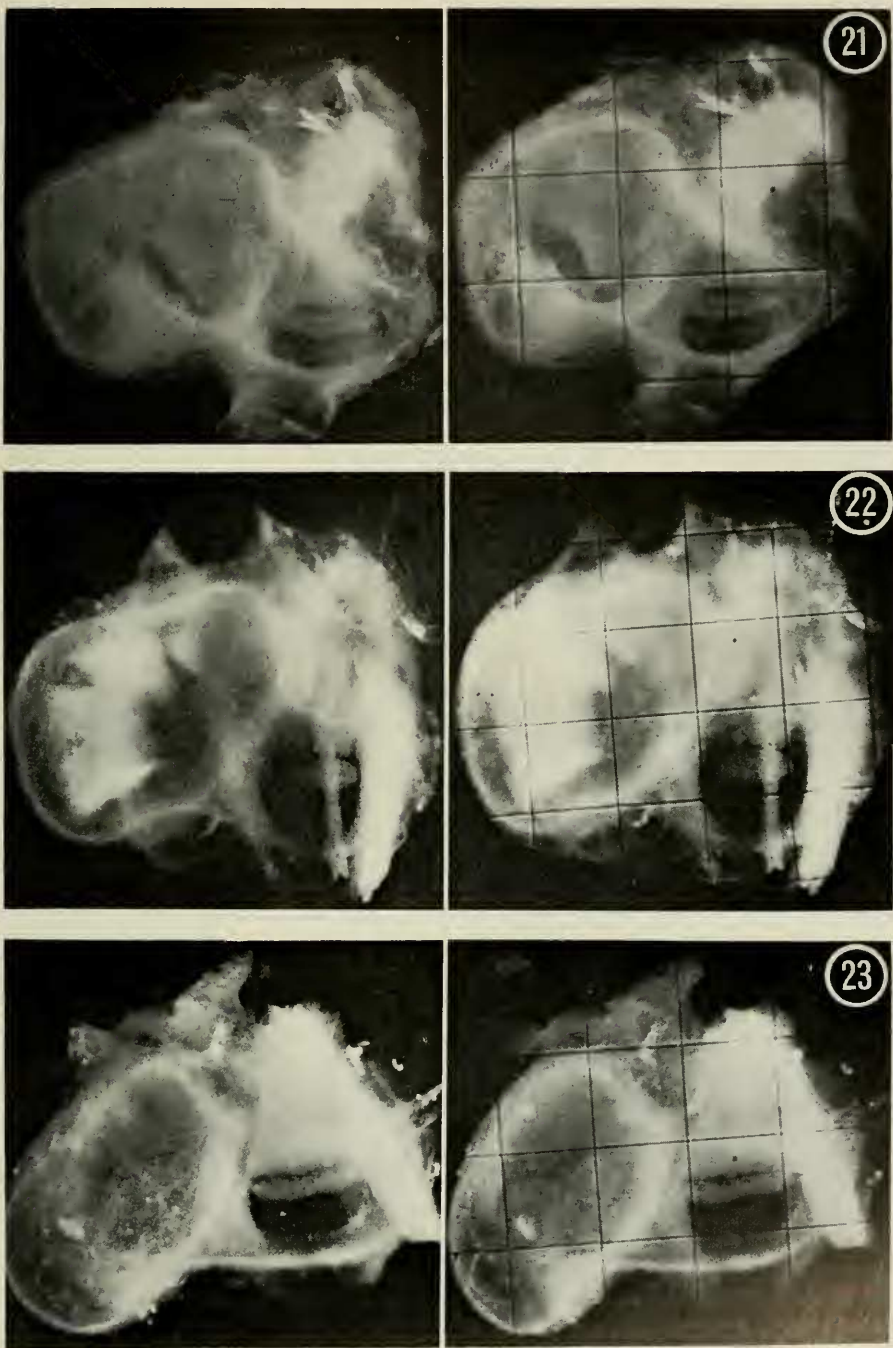
Table X. *Papilla basilaris length and area and limbic/lagenar ratio in the Viperidae.*

Length of papilla basilaris (mm.)		Area of papilla basilaris (mm.²)		Ratio $\dfrac{Area\ limbus}{Area\ lagena}$	
1. *Atheris nitschei*	.21	1. *Sistrurus*	.014	1. *Echis*	.32
2. *Sistrurus catenatus*	.22	2. *Echis*	.016	2. *Sistrurus*	.35
3. *Causus rhombeatus*	.23	3. *Atheris*	.018	3. *Trimeresurus*	.46
4. *Atractaspis bibroni*	.25	4. *Causus*	.018	4. *Ancistrodon*	.48
5. *Echis carinatus*	.25	5. *Crotalus cerastes*	.018	5. *Cerastes*	.52
6. *Crotalus cerastes*	.26	6. *Atractaspis*	.020	6. *Crotalus cerastes*	.59
7. *Ancistrodon halys*	.29	7. *Cerastes*	.020	7. *Crotalus viridis*	.62
8. *Cerastes cerastes*	.30	8. *Trimeresurus*	.025	8. *Vipera*	.64
9. *Vipera aspis*	.31	9. *Ancistrodon halys*	.026	9. *Ancistrodon contortrix*	.67
10. *Crotalus atrox*	.34	10. *Vipera*	.027	10. *Crotalus atrox*	.74
11. *Crotalus viridis*	.35	11. *Crotalus atrox*	.027	11. *Causus*	.76
12. *Trimeresurus gramineus*	.35	12. *Crotalus viridis*	.029	12. *Bitis*	.78
13. *Ancistrodon contortrix*	.48	13. *Ancistrodon contortrix*	.039	13. *Atheris*	.97
14. *Bitis arietans*	.53	14. *Bitis*	.056	14. *Atractaspis*	1.42

There are no distinctive viperid cochlear duct features, but in general, the bony temporal anatomy and the general dimensions of the viperid cochlear duct seem more similar to that of the colubrid than to any other group of snakes.

Elapidae (figs. 24–28, 34 and 35; table XI).

As in burrowing colubrids, the smaller and more secretive elapids have shorter more upright quadrates and shorter stapes, while larger terrestrial species have more angulated quadrates, and longer thinner stapes. The circumfenestral crest is usually more overgrown in elapids than in colubrids, is partially closed in terrestrial elapid species, and almost closed over in smaller secretive species. The stapes footplate is generally large, flat and thin and the juxtastapedial sinus large. The recessus scalae tympani is also large.

A strictly qualitative characteristic of the elapid cochlear duct is the elongate shape of the limbus. Even in those species with a well developed lagenar sac, the limbus is elongate. As is true for snakes in general, the length and area of the papilla tends to increase with body size.

→

FAMILY ELAPIDAE
Dendroaspis species (CAS [665])

FIGURE 24. Lateral aspect. A relatively small sacculus lies above (dorsal to) the cochlear duct. The reunient duct (DR) (sacculo-cochlear) duct is seen in the upper right-hand portion of the field. The limbus of this species is somewhat more ovoid and less elongate than that of most other elapid snakes. Compare with Figs. 34 and 35. ×40.

FIGURE 25. Medial aspect. The large nerve running across the top of the picture is the nerve to the posterior ampulla. The small nerve bundles supplying the papilla and the macula lagenae are well demonstrated. × 40.
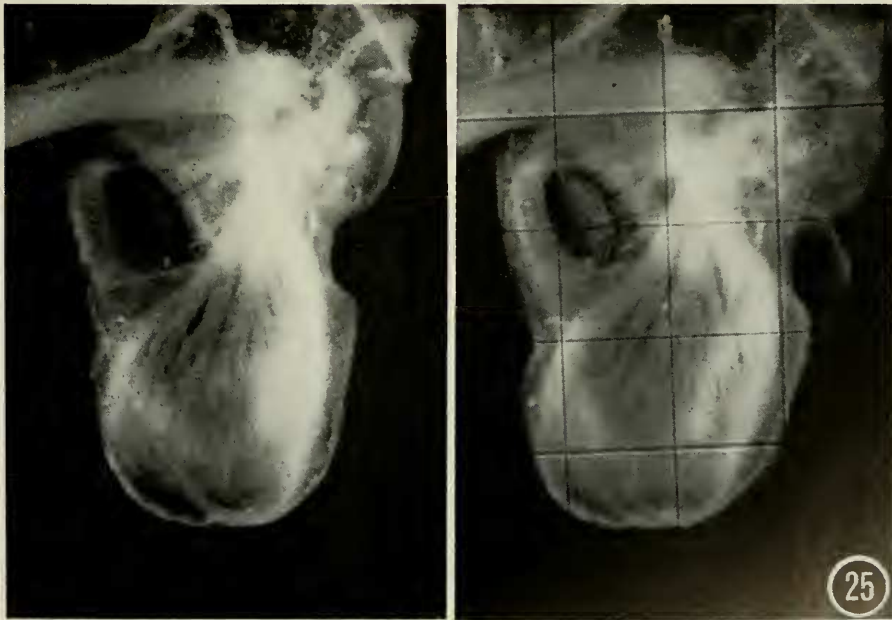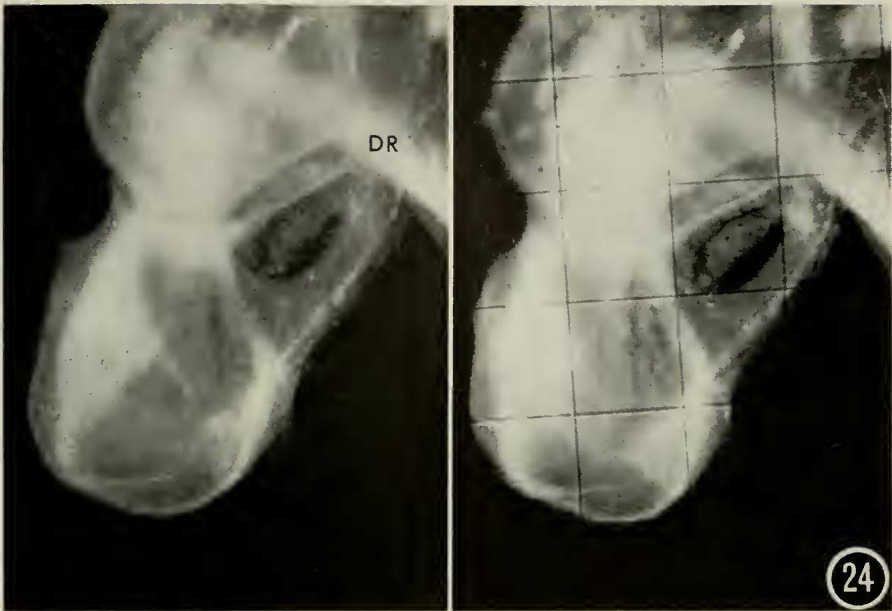
Table XI. *Papilla basilaris length and area and limbic/lagenar ratio in the Elapidae.*

Length of papilla basilaris (mm.)		Area of papilla basilaris (mm.²)		Ratio $\dfrac{Area\ limbus}{Area\ lagena}$	
1. Micruroides euryxanthus	.19	1. Micruroides	.012	1. Dendroaspis	.52
2. Pseudapistocalamus nymani	.26	2. Rhynchoelaps	.016	2. Ophiophagus	.64
3. Calliophis calligaster	.27	3. Demansia	.020	3. Naja melanoleuca	.64
4. Demansia textilis	.29	4. Calliophis	.021	4. Acanthophis	.65
5. Furina annulata	.31	5. Pseudapistocala-		5. Notechis	.67
		mus	.023		
6. Rhynchoelaps bertholdi	.32	6. Furina	.025	6. Demansia	.67
7. Brachyurophis australis	.35	7. Brachyurophis	.028	7. Brachyurophis	.73
8. Dendroaspis species	.38	8. Acanthophis	.032	8. Rhynchoelaps	.78
9. Notechis scutatus	.38	9. Dendroaspis	.033	9. Naja nigricollis	.78
10. Acanthophis antarcticus	.38	10. Notechis	.033	10. Pseudechis	.80
11. Denisonia nigricens	.39	11. Denisonia	.035	11. Denisonia	.97
12. Micrurus fulvius	.43	12. Micrurus	.038	12. Bungarus	1.0
13. Bungarus multicinctus	.44	13. Maticora	.038	13. Micrurus	1.20
14. Walterinnesia aegypti	.47	14. Naja nigricollis	.040	14. Pseudapisto-	
				calamus	1.29
15. Pseudechis porphyriacus	.51	15. Walterinnesia	.040	15. Calliophis	1.33
16. Naja nigricollis	.51	16. Bungarus	.043	16. Walterinnesia	1.33
17. Ophiophagus hannah	.53	17. Pseudechis	.047	17. Maticora	1.35
18. Maticora bivirgata	.54	18. Ophiophagus	.061	18. Micruroides	1.43
19. Naja melanoleuca	.64	19. Naja melanoleuca	.079	19. Furina	1.67

As has been previously mentioned, in the burrowing viperid *Atractaspis*, and the small burrowing colubrids, there has been a marked reduction of the pars lagena in the small burrowing elapids as well. It is not known whether this is related only to the enlargement of the pars limbus, or whether it merely reflects a lack of space in a small skull.

Hydrophiidae (figs. 29, 30, and 35; table XII).

In most species of this family, the stapes has been greatly reduced in size. The circumfenestral crest has almost completely enclosed the small juxtastapedial sinus. The stapes footplate is small and the recessus scalae tympani very reduced in size or absent.

→

Family Elapidae

Figure 26. *Bungarus multicinctus* (CAS [553]). The elongate limbus and papilla of this species is more frequently seen in the elapids than the ovoid type seen in *Dendroaspis*. × 45.

Figure 27. *Naja nigricollis* (CAS [409]). × 30.

Figure 28. *Maticora bivirgata* (CAS [664]). This species shows a markedly elongate limbus and papilla which seems to be characteristic of the more secretive and semi-burrowing elapids. × 45.
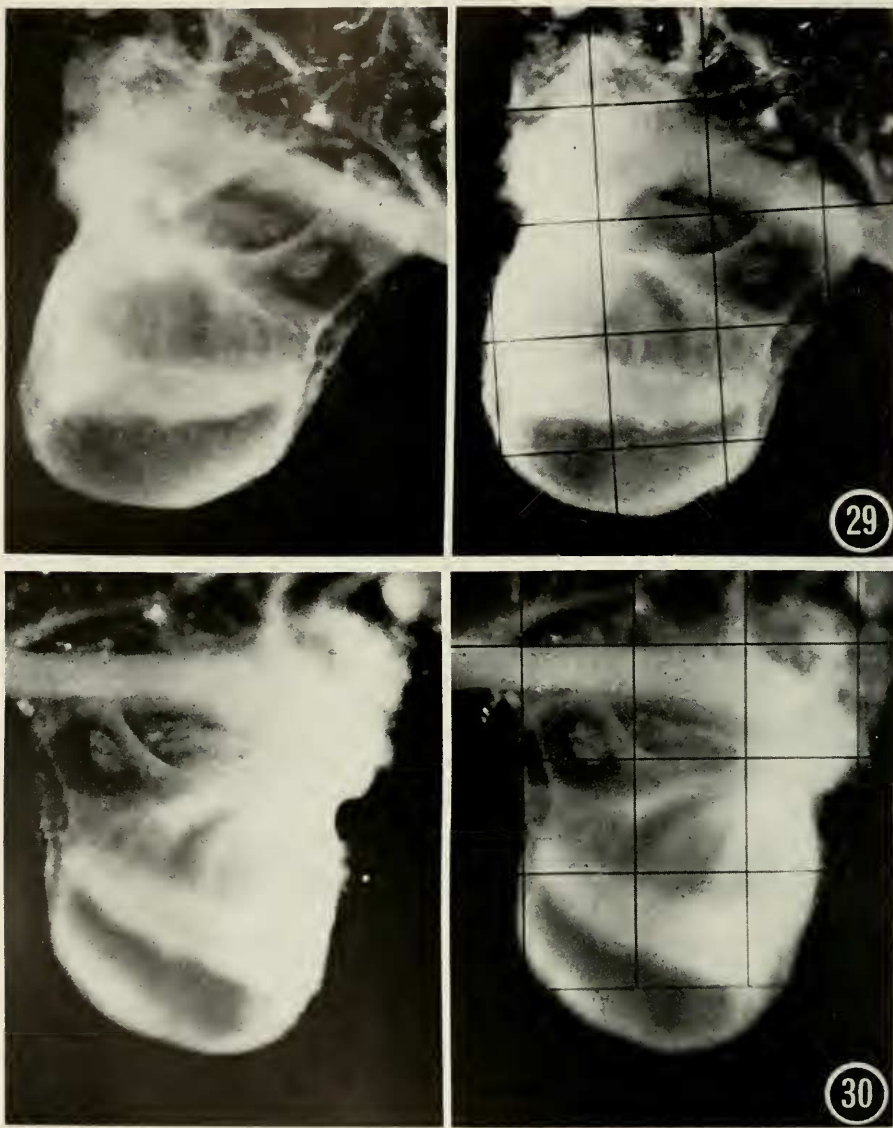
FAMILY HYDROPHIIDAE
Pelamydrus platyurus (CAS [575])

FIGURE 29. Lateral aspect. This cochlear duct is typical of most truly aquatic snakes showing a markedly reduced limbus and papilla. The lagenar sac is large and the macula lagenae clearly demarcated. × 44.

FIGURE 30. Medial aspect. The large nerve running across the upper part of the picture supplies the posterior ampulla. The nerves to the papilla and macula lagenae may also be visualized. × 44.

TABLE XII. *Papilla basilaris length and area and limbic/lagenar ratio in the Hydrophiidae.*

Length of papilla basilaris (mm.)		Area of papilla basilaris (mm.²)		Ratio $\frac{Area\ limbus}{Area\ lagena}$	
1. *Microcephalophis* sp.	.09	1. *Microcephalophis*	.004	1. *Laticauda*	.17
2. *Laticauda colubrina*	.10	2. *Laticauda*	.006	2. *Pelamus*	.22
3. *Aipysurus eudouxi*	.13	3. *Aipysurus*	.008	3. *Lapemis*	.25
4. *Pelamydrus platyurus*	.16	4. *Pelamis*	.011	4. *Enhydrina*	.26
5. *Lapemis hardwicki*	.19	5. *Lapemis*	.013	5. *Microcephalophis*	.30
6. *Enhydrina shistosa*	.21	6. *Enhydrina*	.013	6. *Hydrophis*	.43
7. *Hydrophis melanocephalus*	.21	7. *Hydrophis*	.018	7. *Aipysurus*	.59

In the seven species of hydrophiids studied, there has been absolute reduction in the size of the limbus and papilla basilaris. While a tendency for papillar reduction was observed in aquatic colubrids, only *Herpeton tentaculatum*, *Enhydris pakistanica*, and *Helicops angulatus* have progressed as far as the hydrophiids. Moreover, as in aquatic colubrids, the hydrophiids have cochlear ducts with large lagenar sacs. Again it remains unknown whether the lagena plays some special role under certain conditions or merely enlarges fortuitously when there is a large cochlear recess.

DISCUSSION

The cochlear duct of snakes is probably more primitive than that of any other living reptilian order excepting *Sphenodon*. More detailed descriptions of the cochlear duct of lizards, turtle, and *Sphenodon* are presented by Miller (1966a) but for convenience of the reader summary plates, including illustrations of lizard, turtle, and *Sphenodon* cochlear ducts, are reprinted here (figs. 38 and 39). In many ways the cochlear duct of *Sphenodon* and of snakes are very similar in that there is a simple uncomplicated dorsal limbus to which is appended a ventral lagenar sac. There is little modification of either the lateral or medial face of the limbus. In turtles, on the other hand, there is somewhat closer union between the limbus and lagena, but there are no limbic lips or other modifications. In lizards, the lagena and limbus have been joined into one unified structure and the limbus possesses remarkable alterations of both medial and lateral surfaces. The cochlear duct of crocodilians is considerably more specialized than that of any other living reptile in being more elongate and partially twisted (coiled), and the macula lagenae is reduced to a very small area.

In amphibians, the lagenar sac and the limbus bearing the papilla basilaris are saccular appendages. While these two structures are anatomically contiguous, they are separated by a portion of the sacculus and therefore differ from all reptiles. Thus, a cochlear duct containing both the macula lagenae and papilla basilaris does not appear before the reptilian stage of development, at least in living forms. It is probable that the *Sphenodon* or snake type of cochlear
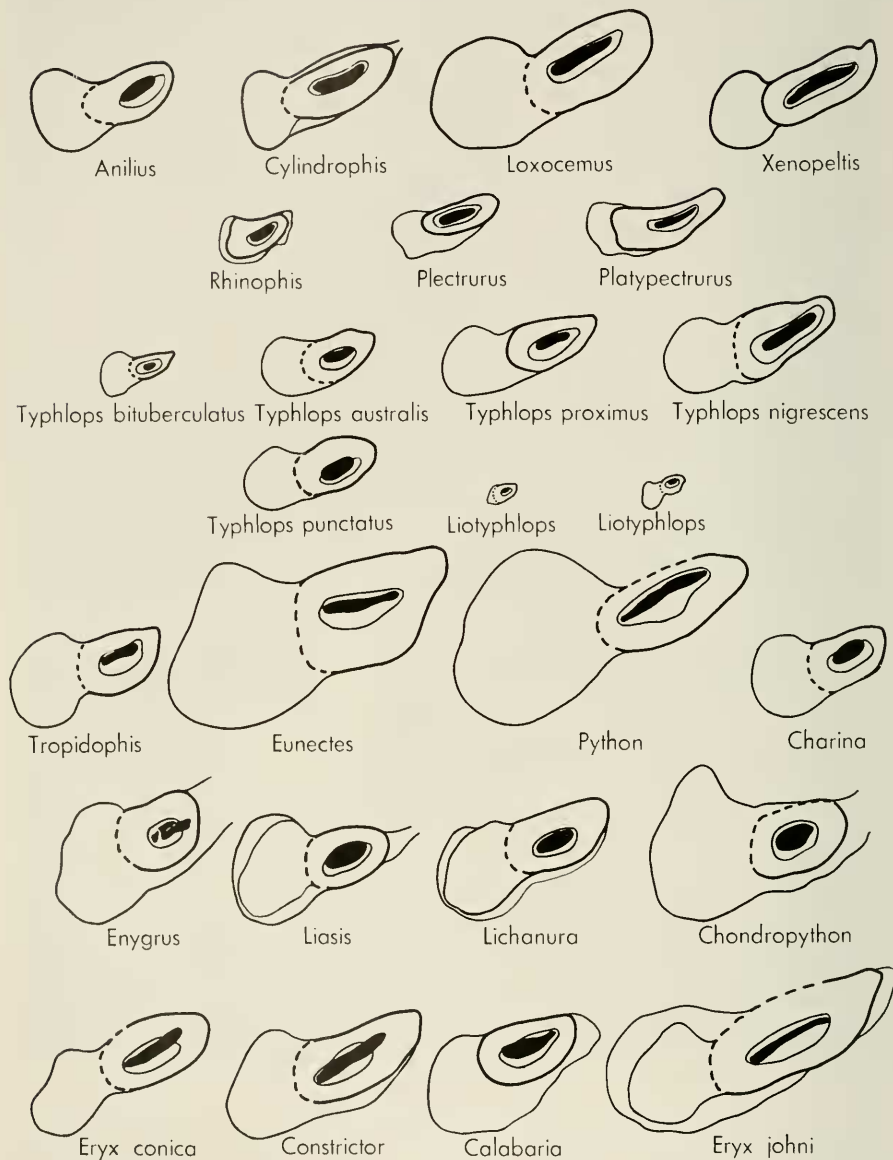
PRIMITIVE FAMILIES

FIGURE 31. Line drawings of the cochlear ducts of species of the more primitive snake families. The species of the genera here figured are listed in table I. All figures were drawn to the same scale. × 14.
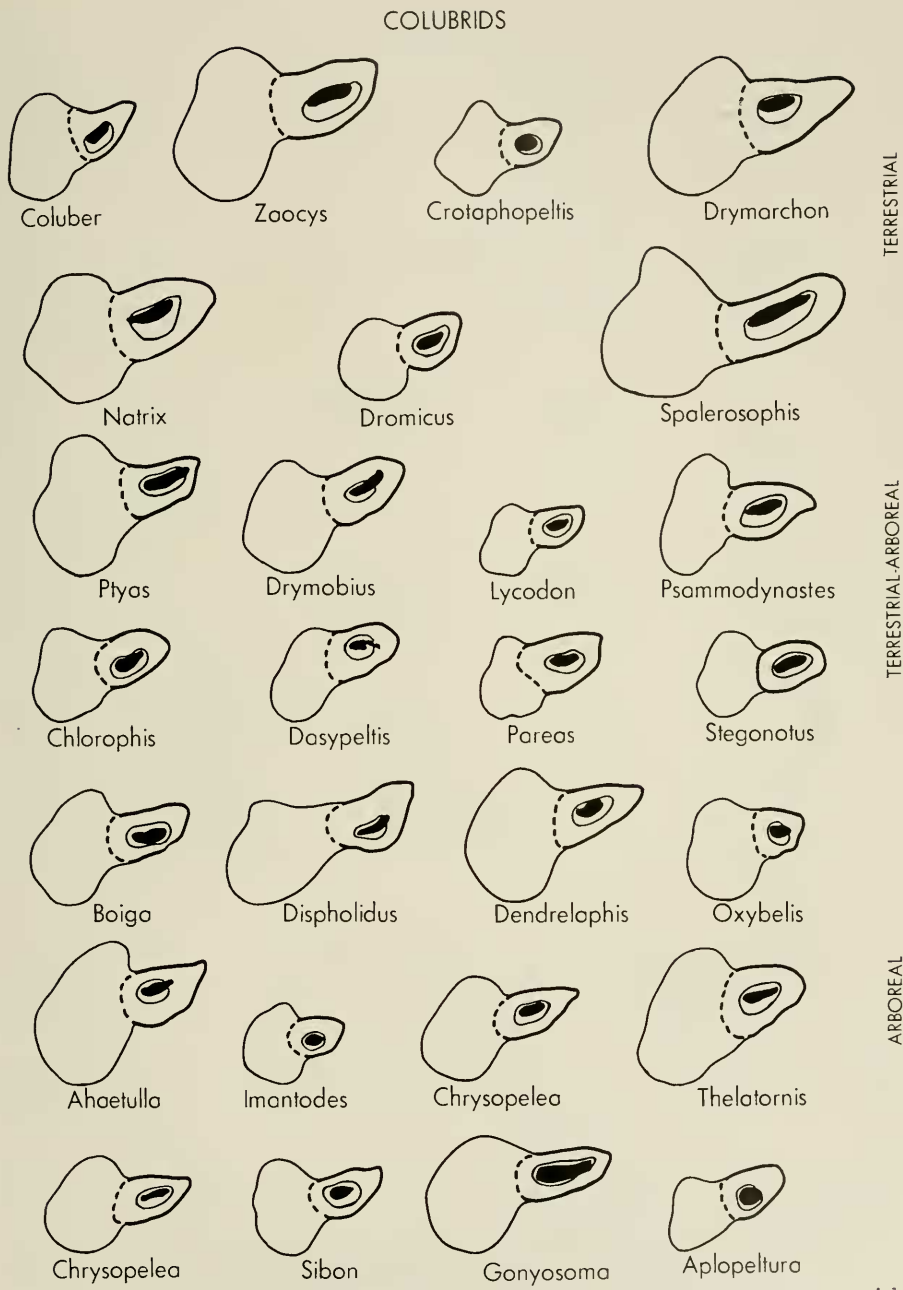
FIGURE 32. Line drawings of the cochlear ducts of species of some terrestrial, terrestrial-arboreal, and arboreal colubrid snakes. The species of the genera here figured are listed in table I. All figures were drawn to the same scale. × 14.
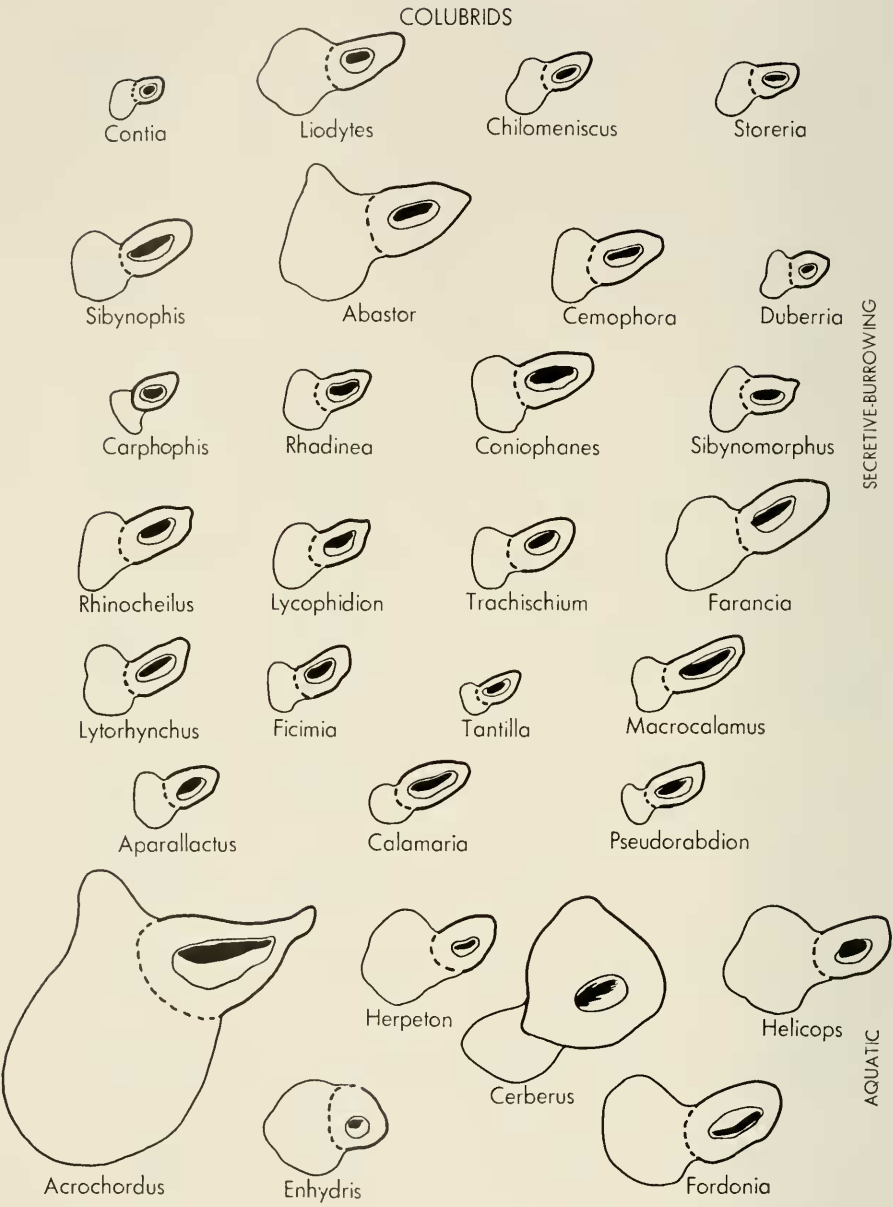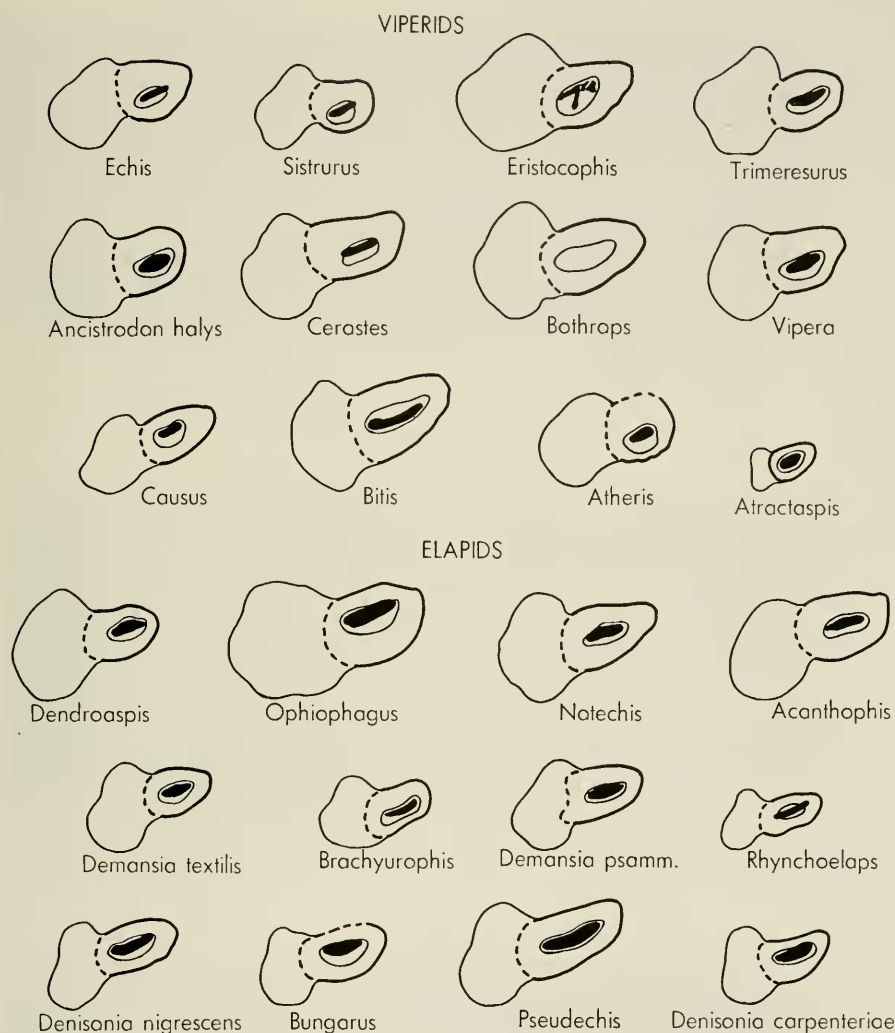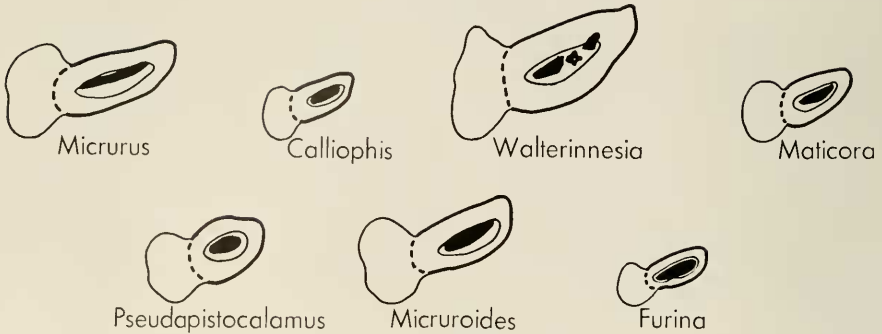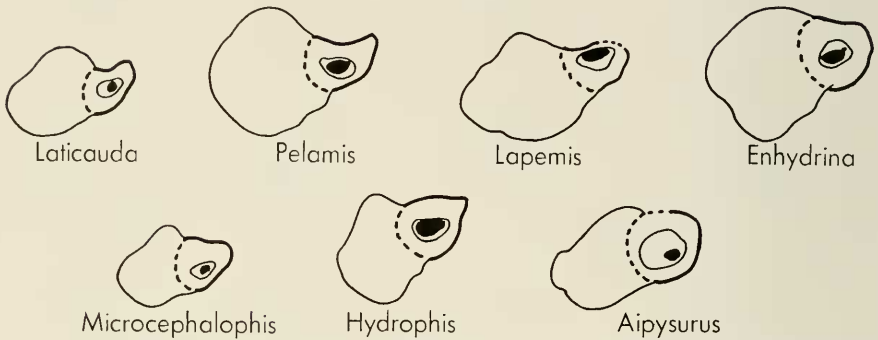
COLUBRIDS

FIGURE 33. Line drawings of the cochlear ducts of species of some secretive-burrowing and aquatic colubrid snakes. The species of the genera here figured are listed in table I. All figures were drawn to the same scale. × 14.

FIGURE 34. Line drawings of the cochlear ducts of species of some viperid and elapid snakes. The species of the genera here figured are listed in table I. All figures were drawn to the same scale. × 14.

duct, where there is relative separation of the pars limbi and lagenae, is more primitive as compared with the conjoined type of duct found in lizards. Retzius (1884) and Hasse (1873) were also of the opinion that among reptiles the cochlear duct of snakes is the simplest or most primitive type.

A detailed study of the cochlear duct of lizards (Miller, 1966a) shows that in certain members of the iguanid-agamid or anguinomorphic groups the duct is not

FIGURE 35. Line drawings of the cochlear ducts of species of some elapid and hydrophiid snakes. The species of the genera here figured are listed in table I. All figures were drawn to the same scale.

highly specialized. However, even these relatively unspecialized cochlear ducts are considerably more advanced than that of *Sphenodon* or snakes. Thus, a close comparison of the cochlear ducts of living snakes and lizards does not clearly indicate probable ancestral relationships. However, on the basis of other anatomical evidence (Bellairs and Underwood, 1951; Underwood, 1967) and the fact that the cochlear ducts of some anguinomorphic lizards are relatively unspecialized, it seems probable that the snake ancestor is to be sought among the primitive anguinomorphs.

It is not possible to make significant comparisons of the functional capacities of various types of reptilian cochlear ducts because so little physiological or behavioral information is available. The only information regarding the auditory capacity of the snake cochlear duct is in reference to cochlear potential studies reported by Wever and Vernon (1960). In three species of terrestrial colubrids
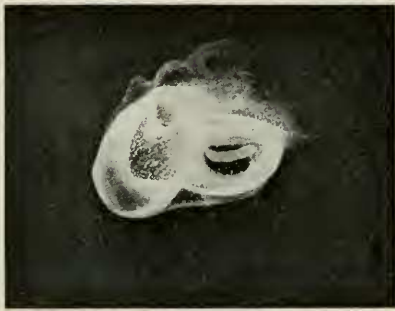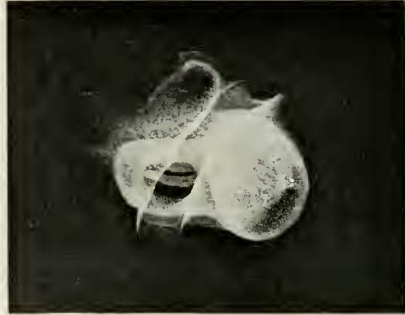
Xenopeltis
(Xenopeltidae)
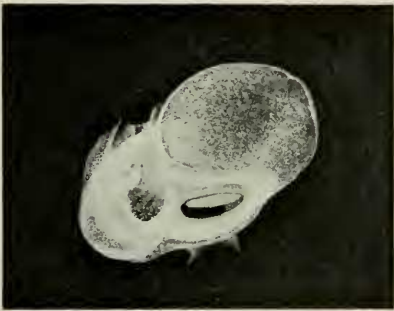
Eryx
(Boidae)

Naja
(Elapidae)

Ancistrodon
(Viperidae)

Pituophis
(Colubridae)

Pelamydrus
(Hydrophiidae)

FIGURE 36. Summary plate showing drawings of the lateral view of the left cochlear ducts of representatives of different snake families. These drawings are not to the same scale.

Xenopeltis
(Xenopeltidae)

Eryx
(Boidae)

Naja
(Elapidae)

Ancistrodon
(Viperidae)

Pituophis
(Colubridae)

Pelamydrus
(Hydrophiidae)

FIGURE 37. Summary plate showing drawings of the medial view of the left cochlear ducts of representatives of different snake families. These drawings are not to the same scale.

(*Pituophis, Thamnophis*, and *Natrix*), the recorded range of greatest sensitivity was from 100 to 500 cps and the degree of sensitivity of the order of –20 decibels. As compared with other types of reptiles, the auditory performance of snakes appears relatively poor.
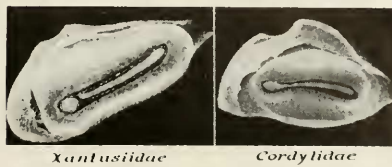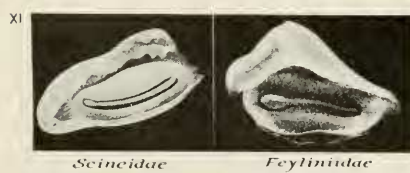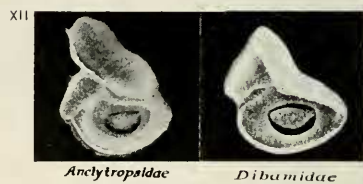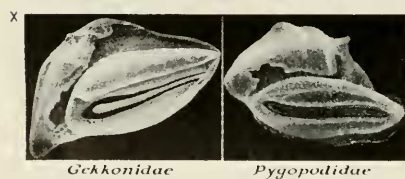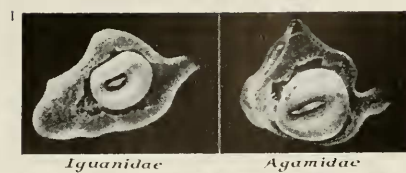
When more physiological information becomes available it is probable that snakes with the longest and largest papillae basilares including the primitive snakes, the boids, and the burrowing elapids and colubrids, will have greater auditory capacities than species with small papillae (particularly aquatic species).

The most pressing unanswered question, however, is the function of the macula lagenae. The fact that the macula lagenae is covered by an otolithic membrane would indicate that its primary role is not auditory. Some evidence (Hamilton, 1963) that the lagenar nerve fibers end in the auditory nuclei, however, engenders caution in estimating the possible function of this structure. Unfortunately, there is no well documented information concerning the behavior of snakes in relation to the auditory sense.

One of the most remarkable characteristics of the snake cochlear duct is the constancy of structural detail throughout this large group of animals. This anatomical consistency is particularly significant when compared to the situation in the lizards where there has been marked diversification of the cochlear duct components. It is possible that the general lack of diversity in snake duct structure is correlated with the absence of both an external and middle ear. Thus, the acoustic sense apparently has not played a significant role in the life and development of snakes. In lizards, on the other hand, the presence of both an external and middle ear has lent greater malleability to the ear as a whole, and selective action has played an important role in the development of the cochlear duct in lizards.

That the ear plays some role in the life of snakes is evident from the observation that the papilla basilaris of most burrowing snakes is better developed than that of other snake types, and conversely, the papillae of arboreal and aquatic snakes is less well developed. It is possible that in the burrowing habitus, the entire body of the snake being in intimate contact with a sound transmitting medium, more sound stimuli are carried to the periotic chambers, and there is a concomitant better development of the papilla basilaris. Apparently in arboreal and aquatic situations, sound stimuli are not as well transmitted to the inner ear, and there has been actual regression of the papillae in these circumstances.

In burrowing lizards, in direct contrast to burrowing snakes, there is regression or degeneration of the acoustic papilla. This is probably so because the lizard cochlear duct was originally developed in relation to a functional external and middle ear, and as these structures degenerated as the animal became burrowing,

Iguanidae   Agamidae

Chamaeleonidae

Anguidae

Anniellidae

Xenosauridae   Helodermatidae

Lacertidae   Teiidae

Varanidae   Lanthanotidae

Gekkonidae   Pygopodidae

Anclytropsidae   Dibamidae

Scincidae   Feyliniidae

Amphisbaenidae   Colubridae

Xantusiidae   Cordylidae

Testudinidae   Sphenodontidae

effective stimuli to the papilla became progressively less, and the papillae in turn underwent regression.

In contrast to the remarkable situation in the lizards where the cochlear duct is a familial diagnostic character, the detailed anatomy of the snake duct is not of marked diagnostic value. However, in some regards, the minor variations in anatomical detail in the cochlear duct are of considerable utility.

One of the most important contributions of this study is the observation that both the extracapsular and intracapsular otic anatomy of various species of *Typhlops* and *Leptotyphlops* is typically ophidian.

The fact that all the members of the primitive snake families Typhlopidae, Leptotyphlopidae, Aniliidae, Loxocemidae, Xenopeltidae, and Uropeltidae have relatively long and large papillae basilares is undoubtedly related to the burrowing habits of these species. The observation that several non-burrowing boids have elongate papillae may indicate that these species were derived from burrowing ancestors, or even that primitive snakes were all burrowing in habitus.

It is possible that the stem snake, which must have arisen at a very early stage from common saurian stock, was a burrowing form without external or middle ear possessing a cochlear duct with a well developed papilla basilaris very much like that of most modern primitive living snakes. As snakes evolved, the burrowers tended to retain a well developed papilla, but in those species of colubrids, elapids, and viperids that lost the burrowing habitus, as the input of sensory information became less the papilla gradually underwent some reduction in size and development.

In cases where a burrowing habitus was redeveloped from a terrestrial ancestor (as in several colubrid species), it is likely that the cochlear duct limbus and papilla basilaris re-elongated. Such an "oscillation" or "reversal" in the degree of development or reduction of an anatomical character may be contemplated in an unspecialized structure such as the snake cochlear duct.

The lizard cochlear duct, on the other hand, has become too specialized to adapt easily to changes in life mode. Thus, when lizards become burrowing, there are degenerative or regressive changes in the ear structure which do not appear to be reversible because of the nature and magnitude of the structural alterations.

←

FIGURE 38. This is a summary plate showing the lateral aspects of the left cochlear ducts of representatives of all living lizard families except the Shinisauridae. For comparative purposes, the cochlear duct of an amphisbaenid, a terrestrial colubrid snake, a turtle, and *Sphenodon* are also shown. The ducts are not drawn to the same scale.

The arrangement does not imply any phylogenetic relationships, but is based on my present concept of the relationships between different lizard families determined in part by anatomical similarities in the cochlear duct and in part by other anatomical affinities. These relationships are discussed in detail elsewhere (Miller, 1966a).
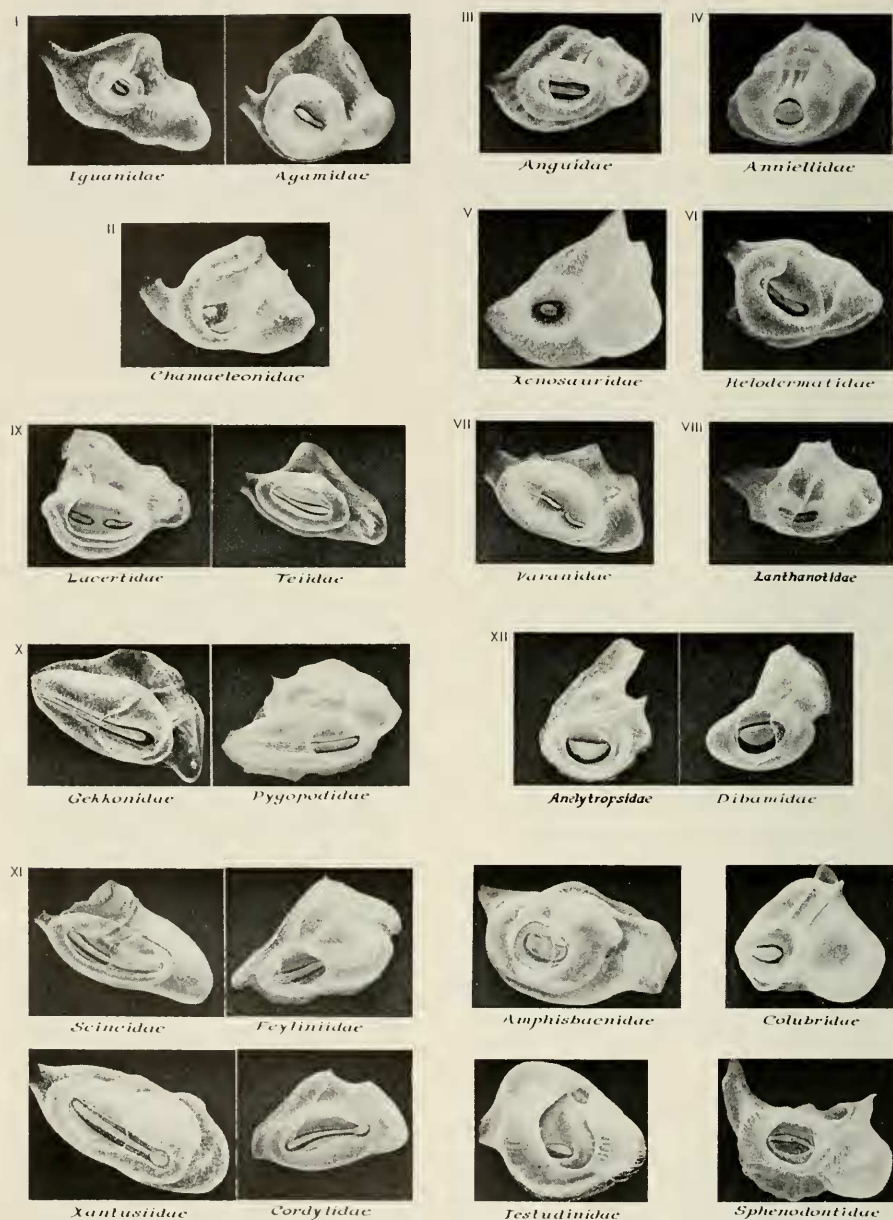
FIGURE 39. Summary plate showing the medial aspect of the left cochlear ducts of different lizard families. For comparative purposes, the cochlear duct of an amphisbaenid, a terrestrial colubrid snake, a turtle, and *Sphenodon* are also shown. The ducts are not drawn to the same scale. For explanation of the arrangement see figure 38.

SUMMARY

The cochlear duct of 200 genera of living snakes has been studied. The snake cochlear duct is a bipartite sac-like structure composed of dorsal limbic and ventral lagenar portions.

The limbus is ovoid to elongate in shape and the papilla basilaris, supported by the basilar membrane stretched across the limbic hiatus, is correspondingly ovoid or elongate. There are no special modifications of either the lateral or medial aspects of the snake limbus.

The lagenar sac is somewhat constricted from the limbic portion of the duct, but the lumina of the pars limbus and lagena are always confluent. A band-like macula lagenae curves about the midportion of the luminal lagenar wall on its caudal, medial, and anterior aspects. The lagenar sac varies considerably in size.

Unlike the cochlear duct of lizards, variation in anatomical detail of the snake cochlear duct is not clearly related to taxonomic grouping, but is related to specific habitat modifications. Thus, more elongate papillae basilares are found in secretive and burrowing snakes, and less elongate papillae in arboreal species. The papilla basilaris is the smallest in aquatic snakes.

Species of the primitive snake families (Aniliidae, Xenopeltidae, Loxocemidae, Uropeltidae, Typhlopidae, Leptotyphlopidae) are all burrowing snakes and have markedly elongate papillae basilares. The auditory apparatus of typhlopids and leptotyphlopids is typically ophidian. In the Boidae, also a primitive family, most species have elongate papillae, even in those that are not burrowers such as in *Eunectes*, *Python*, and *Constrictor*.

The lagenar sac is often smaller in burrowing species where most of the available space in the cochlear recess is occupied by the elongated limbus. In large species, and frequently in aquatic snakes, the lagenar sac is large.

Very little is known concerning the function of either the papilla basilaris or the macula lagenae in snakes.

It is probable that the cochlear duct of snakes is more primitive than that of turtles, lizards, or crocodiles.

The cochlear duct of any living lizard is considerably more specialized than that of any snake. Thus, it is not possible on the basis of cochlear duct anatomy alone to estimate the closeness of relationship between a particular group of living lizards and snakes.

It is very likely that snakes and lizards arose from a common ancestor very early in saurian history.

Whether or not the snake progenitor was a burrowing form is problematical, but probable.

The cochlear duct of snakes has remained unspecialized to a degree that it is possible that both the papilla basilaris and macula lagenae may increase or decrease in size coincident with habitat modification.

The cochlear duct of lizards, on the other hand, has achieved a degree of specialization that precludes simple alterations of its components coincident with a change in habitus.

ACKNOWLEDGMENTS

LITERATURE CITED

BAIRD, I. L.

 1960. A survey of the periotic labyrinth in some representative recent reptiles. University of Kansas Science Bulletin, vol. 41, pp. 891–981.

BELLAIRS, A. d'A., and G. UNDERWOOD

 1951. The origin of snakes. Biological Reviews, vol. 26, pp. 193–237.

DE BURLET, H. M.

 1934. Vergleichende Anatomie des stato-akustischen Organs. a. Die innere Ohrsphäre; b. Die mittlere *Ohrsphäre. In:* Bolk, Goppert, Kallius, u. Lubosch, Handbuch der vergleichenden Anatomie der Wirbeltiere, II, Part II. Urban and Schwartzenberg, Berlin, pp. 1293–1432.

DOWLING, H. G.

 1959. Classification of the Serpentes: A critical review. Copeia, 1959, No. 1, pp. 38–52.

HAMILTON, D. W.

 1963. Posterior division of the eighth cranial nerve in *Lacerta vivipara.* Nature, vol. 200, pp. 705–706.

 1964. The inner ear of lizards. I. Gross structure. Journal of Morphology, vol. 115, pp. 255–271.

HASSE, C.

 1873. Die vergleichende Morphologie und Histologie des häutigen Gehörorganes der Wirbelthiere. Supplement zu den anatomischen Studien, Band I. Wilhelm Engelmann. Leipzig.

KUHN, A.

 1882. Ueber das häutige Labyrinth der Reptilien. Archiv für mikroskopische Anatomie, vol. XX, pp. 271–361.

MILLER, M. R.

 1966a. The cochlear duct of lizards. Proceedings of the California Academy of Sciences, fourth series, vol. 33, pp. 255–359.

 1966b. The cochlear duct of lizards and snakes. American Zoologist, vol. 6, pp. 421–429.

 1966c. The cochlear ducts of *Lanthanotus* and *Anelytropsis* with remarks on the familial relationship between *Anelytropsis* and *Dibamus.* Occasional papers of the California Academy of Sciences, no. 60, 15 pp.

RETZIUS, G.

 1884. Das Gehörorgan der Wirbelthiere. II. Das Gehörorgan der Reptilien, der Vögel, und der Säugethiere. Samson and Wallin, Stockholm, 368 pp., 39 pl.

SCHMIDT, R. S.
  1964.   Phylogenetic significance of the lizard cochlea. Copeia, pp. 542–549.
SHUTE, C. C. W., and A. D'A. BELLAIRS
  1953.   The cochlear apparatus of Gekkonidae and Pygopodidae and its bearing on the
          affinities of these groups of lizards. Proceedings of the Zoological Society of
          London, vol. 123, pp. 695–709.
SMITH, M. A.
  1943.   The Fauna of British India, Ceylon and Burma. Reptilia and Amphibia. Vol. III
          —Serpentes. 583 pp. Taylor and Frances, London.
TAYLOR, E. H.
  1922.   The snakes of the Philippine Islands. Department of Agriculture and Natural
          Resources, Bureau of Science, Manila. Publication No. 16, 312 pp.
UNDERWOOD, G.
  1967.   A Contribution to the Classification of Snakes. Trustees of The British Museum
          (Natural History), London. Publication No. 653. 179 pp.
WALLS, G. L.
  1942.   The Vertebrate Eye. Cranbrook Institute, Bloomfield Hills, Michigan.
WEVER, E. G., and J. A. VERNON.
  1960.   The problem of hearing in snakes. Journal of Auditory Research, vol. 1, pp.
          77–83.